ZooKeys 952: 1–63 (2020)
doi: 10.3897/zookeys.952.50617
https://zookeys.pensoft.net

MONOGRAPH

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Ceriantharia (Cnidaria) of the World: an annotated catalogue and key to species

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Academic editor: B. W. Hoeksema | Received 28 February 2020 | Accepted 12 May 2020 | Published 23 July 2020

http://zoobank.org/96103618-0C3A-4DE9-BCC1-9AE0A824B9D8

Citation: Stampar SN, Reimer JD, Maronna MM, Lopes CSS, Ceriello H, Santos TB, Acuña FH, Morandini AC (2020) Ceriantharia (Cnidaria) of the World: an annotated catalogue and key to species. ZooKeys 952: 1–63. https://doi.org/10.3897/zookeys.952.50617

Abstract

The diversity of Ceriantharia is known from studies formally describing species from the late 18th Century onwards. However, no nomenclators including a list and discussion of all valid species have been produced since a list discussed by Carlgren in 1912. The present nomenclator presents a complete list of adult species of Ceriantharia of the World, including a discussion on each species. It includes the three families (Arachnactidae, Botrucnidiferidae, Cerianthidae) and the currently accepted 54 species based on their adult form. This study serves as a presentation of the "state-of-the-art" list of species of Ceriantharia, and includes a species identification key to support taxonomic identification. Additional in-depth species-by-species investigations for almost all cerianthid species is still needed, as the information available for most of these species is quite superficial.

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Keywords
Cnidaria, families, genera, identification key, tube-dwelling anemones

Introduction

The subclass Ceriantharia Perrier, 1893 (Fig. 1), a group of anthozoan species commonly known as 'tube anemones', is characterized by the presence of two tentacle discs and a tube produced by filaments of a special kind of cnida, the ptychocyst (Daly et al. 2007; Stampar et al. 2016). This group of sediment-dwelling species is recognized as some taxa are common as pets in the aquarium industry (Stampar and Silveira 2006). On the other hand, the general taxonomy of the group is rather confusing, and the literature includes some incorrect definitions of characters for both species and genera (Torelli 1961; Stampar et al. 2012; 2016).

Knowledge on Ceriantharia dates back from the late 1700s, with the description by Spallanzani (1784) of an aberrant and tubular hydroid species with a membranous tube around the body, *Tubularie* (= *Tubularia membranosa* in Gmelin, 1791: 3836). Currently, the subclass Ceriantharia is divided into three families, eight genera, and includes 54 valid species (den Hartog 1977; Stampar et al. 2016; Molodtsova 2020) (Fig. 2). Different Ceriantharia classification schemes exist, with only limited consistency with each other (e.g., Mejia et al. 2019). However, until now, there has been only one published table-style catalogue (= nomenclator) of all species of tube-anemones, which is over a century old (Carlgren 1912a) and does not contain an extensive bibliographic compilation. Additionally, many species descriptions (e.g., Arai 1965; Molodtsova 2001a) and higher-level taxonomic reorganizations have taken place since 1912, and, thus, subsequent researchers have faced difficulties in finding and organizing historical and recent citations and information on Ceriantharia. Therefore, there is an obvious need for an organized species nomenclator, as well as for an identification key to aid in further studies of this group. Here, we present a nomenclator and a key to the extant valid Ceriantharia species in their adult form (polyps), including discussions of the status of each species. Some other articles have addressed larval forms (Molodtsova 2004b; Stampar et al. 2015b) but these are not included in the present study.

Material and methods

The checklist's classification follows den Hartog (1977) for the orders and Carlgren (1912b, 1931) for genera of the subclass Ceriantharia. Cited articles have mostly been compiled from specific literature. The online databases Hexacorallians of the World (Fautin 2013) and the World Register of Marine Species (Molodtsova 2020)

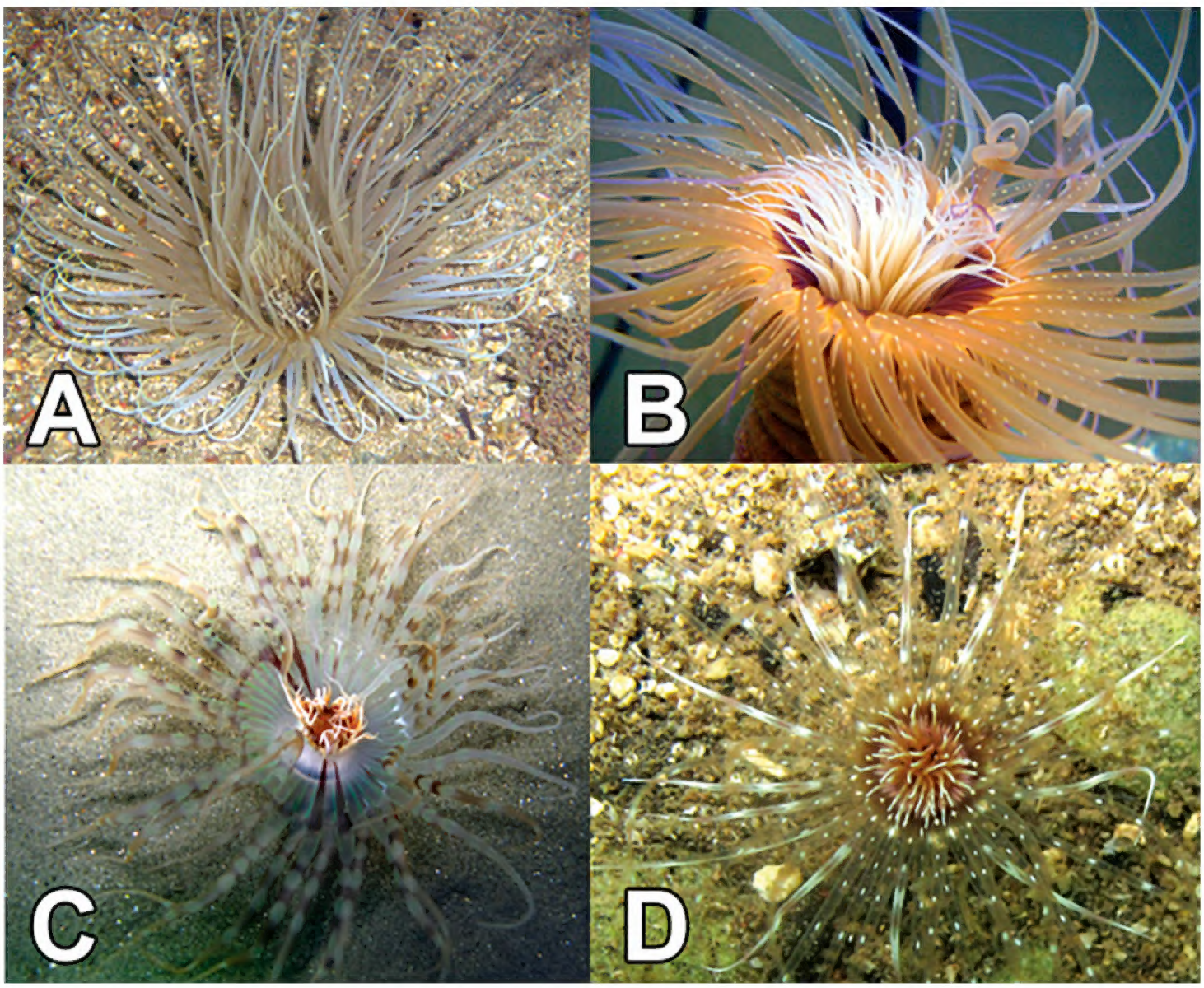

Figure 1. Examples of Ceriantharia: **A** Cerianthidae, *Ceriantheomorphe brasiliensis* **B** *Pachycerianthus schlenzae* **C** Arachnactidae, *Isarachnanthus nocturnus* **D** Botrucnidiferidae, *Botruanthus mexicanus* (Photograph Ricardo Gonzalez-Muñoz).

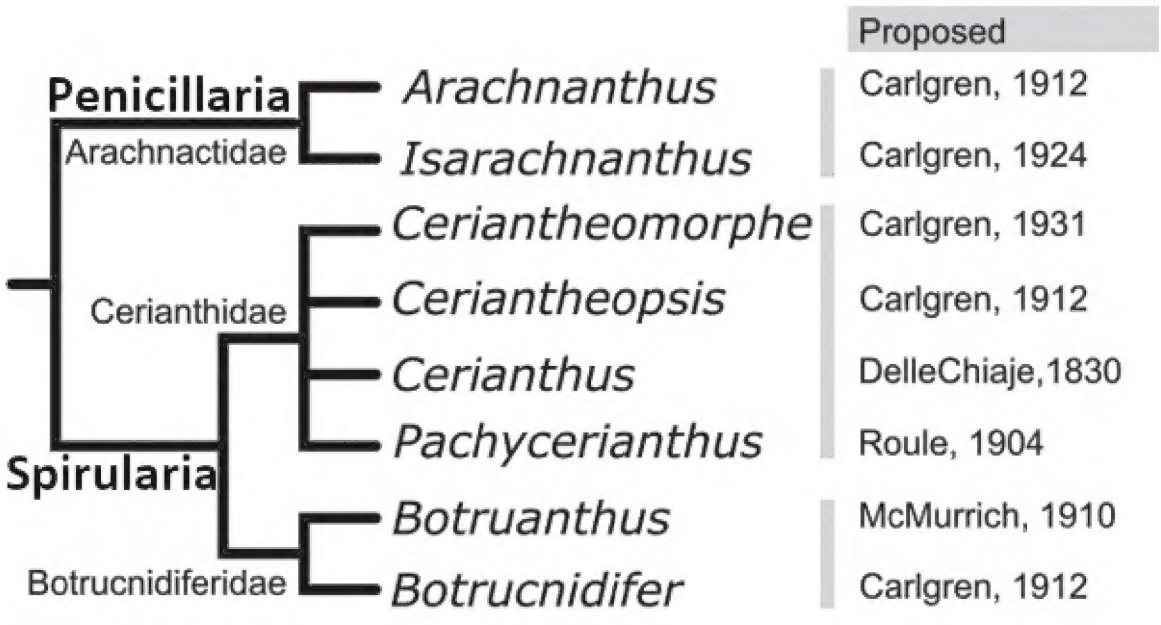

Figure 2. Classification of Ceriantharia (adapted from Stampar et al. 2016a).

were used to assist in bibliographic compilations. Information on deposited specimens was obtained directly from the original descriptions and/or collections of mentioned museums for each species. If the type material was not found, this information is indicated for each species. In terms of life cycle, larval forms of cerianthids were not added to this study, as it is still not possible to make proper correlations with adult forms without the aid of molecular-based re-examinations (e.g., Stampar et al. 2015c). The identification key was constructed with the characters available for each species, although unfortunately some species have sparse descriptions and only a few distinctive characters are known.

Results

The compilation of species resulted in a list of 54 valid species (Fig. 2) of adult forms of Ceriantharia. The current classification divides the species into the families Arachnactidae (nine species, 16%); Botrucnidiferidae (four species, 8%), and Cerianthidae (41 species, 76%). There is a clear prevalence in numbers of Cerianthidae species, and this can be explained by the large sizes and high visibility of many species described in this family (Stampar et al. 2016). There are two clear periods of comparatively high rates of formal species descriptions with a long break in between them (Fig. 3): a) the 'Carlgren/van Beneden/McMurrich period' (1890 to 1951), and b) the 'Molodtsova/Stampar period' (ongoing from 2001). During these two periods more than 75% of the valid Ceriantharia species were described.

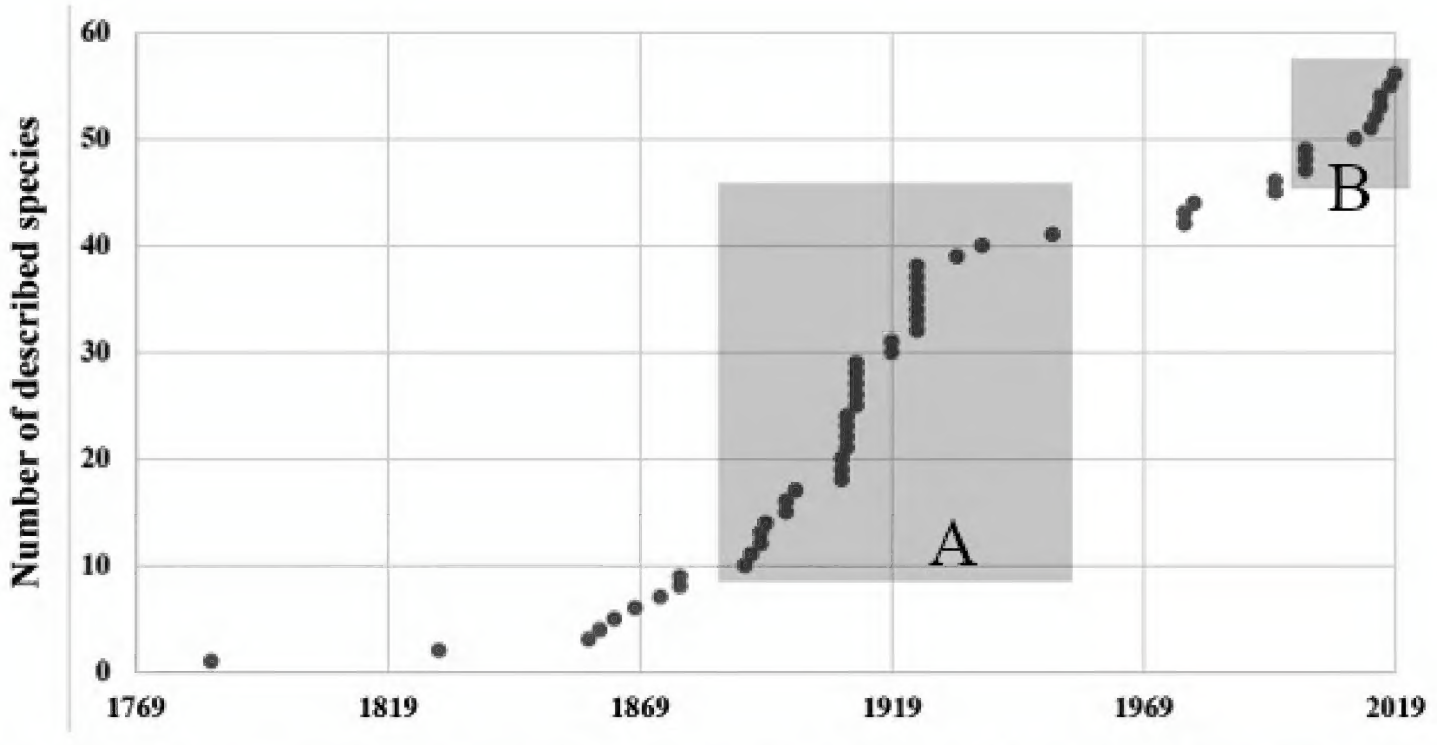

Figure 3. The cumulative number of Ceriantharian species descriptions per year. **A** Period Carlgren/van Beneden/McMurrich (1890 to 1951) and **B** Period Molodtsova/Stampar (2001 to present).

Checklist

Phylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834
Subclass Ceriantharia Perrier, 1893
Order Spirularia den Hartog, 1977

Number of valid taxa: two families, six genera, and 45 species

Family Cerianthidae Milne Edwards & Haime, 1851

Number of valid taxa: four genera and 41 species

Genus *Ceriantheomorphe* Carlgren, 1931

Table 1

Type species. *Ceriantheomorphe brasiliensis* by original designation (Carlgren 1931).

Number of valid species: 3

1 *Ceriantheomorphe ambonensis* (Kwietniewski, 1898)

http://zoobank.org/A5A81C1F-3180-4114-A624-E9F1CDA889B5

Cerianthus ambonensis Kwietniewski, 1898: 426; Pax 1910: 167; McMurrich 1910: 26–28 Carlgren 1912a: 44–47; Lopes et al. 2019: 127–148
(?) *Cerianthus sulcatus* McMurrich, 1910: 28–30
Ceriantheomorphe ambonensis: Carlgren 1931: 1

Type locality. Moluccas (Maluku) Islands, Indonesia, shallow waters.

Distribution. Only known from shallow water at the type locality.

Remarks. The original description made by Kwietniewski (1898) is very simple and based only on external characters. McMurrich (1910) obtained two specimens from the same area and conducted a more detailed anatomical study. Carlgren (1931), based on McMurrich's description, moved the species to the newly erected genus *Ceriantheomorphe*. There has been no other subsequent research performed on this species. This species is commercially exploited for the international aquarium trade (exported from Indonesia), perhaps owing to its vivid orange color (S. Stampar pers. obs.).

Type material. Not found in this study.

Table 1. Comparison of anatomical features of *Ceriantheomorphe* species (after Lopes et al. 2019).

	C. ambonensis	*C. brasiliensis*	*C. adelita*
Marginal tentacles	More than 100	Up to 392	Up to 352
Directive labial tentacle	Absent	Present	(?)
Arrangement of labial tentacles	(0)112.2112	(1)123.1324.3124.3124	(?)112.211
Actinopharynx	1/8 to 1/10 of gastric cavity	1/4–1/5 of gastric cavity	1/7 to 1/8 of gastric cavity
Oral disc	~ 4 cm	~5 cm	~3 cm
Siphonoglyph	Long, 6 mesenteries attached	Rather wide, 4 mesenteries attached	Long, 6 mesenteries attached
Directive mesenteries	>Actinopharynx	>Actinopharynx	>Actinopharynx
P2	Almost to aboral pole	To aboral pole	Almost to aboral pole
P3	Short, ≅ directives	Short, < directives	Short, > directives
M	± 2B	± 2B	± 2B
M3	± M2	=M2	± M2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present	Present
Craspedion tract at fertile mesenteries	2/4	2/5 – 3/5	2/5 – 3/5

2 *Ceriantheomorphe brasiliensis* (Mello-Leitão, 1919)

http://zoobank.org/6336C2A6-B8DB-4B0F-9137-3525DCE698D6

(?) *Cerianthus americanus*: Hertwig, 1882: 110 116

Cerianthus brasiliensis Mello-Leitão, 1919: 38–39

Ceriantheomorphe brasiliensis: Carlgren 1931: 2–6; Carlgren 1940: 6,11–12; Stampar et al. 2010: 205–209; Silveira and Morandini 2011: 3; Rodriguez et al. 2011: 52, 54–55; Spier et al. 2012: 1–3; Stampar et al. 2012: 5–6, 9; Stampar et al. 2014a: 2,5,8; Stampar et al. 2014b: 344, 347, 351, 353; and Stampar et al. 2015a: 3; González-Muñoz et al. 2016: 5, 9; Stampar et al. 2016: 64, 67, 68; Stampar and Morandini 2017: 690; Lopes et al. 2019: 127–148

(?) *Cerianthromorphe brasiliensis*: Hedgpeth 1954: 286

Type locality. Baía de Guanabara, Rio de Janeiro, Brazil.

Distribution. Brazil (Espírito Santo (20.5°S) to Rio Grande do Sul (33.7°S) states); Uruguay (35°S), and Gulf of Mexico (dubious record, 24–29°N), shallow waters (at < 40 m depth).

Remarks. This species was first described as *Cerianthus brasiliensis* by Mello-Leitão (1919) from Guanabara Bay, Rio de Janeiro, Brazil. This description is quite simple and based on only a few external morphological characters. Oskar Carlgren visited the Museu Nacional do Rio de Janeiro (MNRJ) at the time of description of the genus *Ceriantheomorphe* sometime between 1925 and 1929, but he was unable to find the type material designated by Mello-Leitão. However, the type material (MNRJ 100) of *Cerianthus brasiliensis* is available and, based on our examinations, every mesentery, except for the directives, is fertile. Thus, based on this, the species described by Mello-Leitão should

be moved to the genus *Ceriantheomorphe*. Carlgren (1931) mentions that the species (with this name) as described by him in that publication may be a junior synonym of *C. brasiliensis* Mello-Leitão 1919, as Lopes et al. (2019) have shown. Hertwig (1882) recorded a specimen of *Cerianthus americanus* from the Uruguayan coast whose external shape appeared to be very similar to that of *Ceriantheomorphe brasiliensis*. However, that specimen was not available at the time of the present study and may be lost.

Type material. Museu Nacional do Rio de Janeiro – MNRJ 100 (Holotype).

3 *Ceriantheomorphe adelita* Lopes, Morandini & Stampar in Lopes et al., 2019

http://zoobank.org/702bdfdd-870c-43eb-b59a-05a994177d56

Ceriantheomorphe adelita Lopes et al., 2019: 127–148
Cerianthromorphe brasiliensis: Molodtsova 2009: 365–367
(?) *Cerianthromorphe brasiliensis*: Carlgren and Hedgpeth 1952: 148, 169–170; Hedgpeth 1954: 286; 290; Frey 1970: 309

Type locality. off Port Aransas, 32 km south off Corpus Christi, Texas, United States of America.

Distribution. Gulf of Mexico (Northern Mexico) to North Atlantic (North Carolina, United States of America), shallow waters.

Remarks. A very large species, which for many years was considered to be synonymous with *C. brasiliensis* even without biogeographic justification. Recently, Lopes et al. (2019) have indicated morphological differences that support the distinction between both species. Apparently, this is a species with very low incidence, since several sampling attempts have been unsuccessful (S. Stampar pers. obs.).

Type material. Smithsonian National Museum of Natural History NMNH 50015 (holotype).

Genus *Ceriantheopsis* Carlgren, 1912

Table 2

Type species. *Ceriantheopsis americana* by original designation (Carlgren 1912a)
Number of valid species: 4

4 *Ceriantheopsis americana* (Agassiz in Verrill, 1864)

http://zoobank.org/a5de3b9f-56d7-4f46-a5ff-56a01f2c132a

Cerianthus sp. Agassiz 1859: 24
Cerianthus americanus Agassiz in Verrill, 1864b: 32–33; Verrill 1864a: 56–57; Verrill 1872: 436; Hertwig 1882: 110,116; Andres 1883: 352; McMurrich 1887: 63; van Beneden 1897: 140; Haddon 1898: 401; Parker 1900: 756; Duerden 1902a: 329–

Table 2. Comparison of anatomical features of *Ceriantheopsis* species (after Stampar et al. 2016).

	C. americana	*C. nikitai*	*C. austroafricana*	*C. lineata*
Marginal tentacles	Up to 100–120	Up to 70	Up to 70	Up to 60
Directive labial tentacle	Present	Present	Present	Absent
Arrangement of labial tentacles	(2)413.4232.4312* (4)413.4231.4312.4312	(3)423.4232.4312.4312	(2)313.4343.4324.3124	4231.4231.4231.4231
Actinopharynx	1/12–1/8 of gastric cavity	1/5–1/4 of gastric cavity	1/10–1/8 of gastric cavity	1/6-1/5 of gastric cavity
Oral disc	0.7–1.0 cm	~0.6–0.7 cm	Wide, ~1.5 cm in preserved	1.0 – 1.5 cm in preserved
Siphonoglyph	Narrow, 4 mesenteries attached	Wide, 4 mesenteries attached	Wide, 4 mesenteries attached	Narrow, 2 mesenteries attached
Directive mesenteries	<Actinopharynx	~Actinopharynx	~Actinopharynx	<Actinopharynx
P2	To aboral pole	To aboral pole	To aboral pole	Almost to aboral pole
P3	=B	=B	=B	=B
M	>>B	<2B	>B	≥B
M3	≤M2	>M2	≤M2	<Half M2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Not present	Present	Present
Craspedion tract at fertile mesenteries	6/7–8/9	3/5	6/7	~6/7-8/9
Cnido-glandular tract at B	<<b	=b	<b	<b
Craspedonemes of craspedion at fertile mesenteries	Sometimes present	Absent	Absent	Absent

330; Duerden 1902b: 301; Roule 1905: 89; McMurrich 1910a: 11,15–16,20; Hargitt 1912: 249; Mello-Leitão 1919: 36–38; van Beneden 1924: 91; Field 1949: 5–6, 18–21, 27; den Hartog 1977: 212; Pei 1998: 179–180

Ceriantheopsis americanus: Carlgren 1912a: 366; Carlgren 1912b: 19–26; Pax 1924: 118; Carlgren 1940: 6, 12–13; Leloup 1964: 257; Frey 1970: 309–311; Peteya 1973a: 301–316; Peteya 1973b: 1–10; Widersten 1976: 858; Shepard et al. 1986: 625–646; Kristensen et al. 1991: 590–591, 589–614; Sebens 1998: 13, 16, 21, 57; Holohan et al. 1998: 466–468; Molodtsova 2000: 14,17; Molodtsova et al. 2011: 2–3, 5–7; Reft and Daly 2012: 123–125, 127, 129; Mata et al. 2012: 602–603; Kayal et al. 2013: 3, 5–6, 10–11, 15; Stampar et al. 2014a: 2, 8

Cerianthiopsis americanus: Hedgpeth 1954: 286–290

Ceriantheopsis americana: Stampar et al. 2015b: 1–6; Stampar et al. 2016a: 69

Type locality. Off Charleston, South Carolina; Beaufort, North Carolina, United States of America (not specified).

Distribution. Atlantic coast of United States and Canada, Gulf of Mexico, and Caribbean Sea, at 2–250 m depth.

Remarks. This species is probably the most extensively studied among the Ceriantharia. There are appropriate descriptions of specimens (McMurrich 1910; Carlgren 1912a) and there is much biological information, especially related to ecological aspects (Shepard et al. 1986; Kristensen et al. 1991; Holohan et al. 1998). One important issue that still needs be studied is the possible occurrence of this species in the deep sea. Several photographic records, especially from ROV surveys below 400 m depth are available on the internet, but, to date, no such deep specimens have been collected for study.

Type material. Museum of Comparative Zoology (Harvard) – Invertebrate Zoology 243 and SCOR-1245 and Peabody Museum of Natural History (Yale) – YPM IZ 000977.CN (syntype).

5 *Ceriantheopsis austroafricanus* Molodtsova, Griffiths & Acuña, 2011

http://zoobank.org/5E824C53-474E-4822-B48E-EA47D6801DC0

Ceriantheopsis austroafricanus Molodtsova et al., 2011: 1–7; Stampar et al. 2015b: 1–3, 6

Type locality. Off Cape Town, South Africa.

Distribution. Only known from shallow waters at the type locality (8–15 m depth).

Remarks. This species was recently described and therefore little is known about it beyond a detailed morphological description. One of the most interesting features of the species is the wide range of colors (Molodtsova et al. 2011). This species occurs in waters around Cape Town. Interestingly, this species is found close to industrialized coastal development, such as marinas and ports (S. Stampar pers. obs.), which may have provided a special habitat.

Type material. Zoological Museum of Moscow State University – ZMMU No. Ec-105 (holotype).

6 *Ceriantheopsis lineata* Stampar, Scarabino, Pastorino & Morandini, 2015

http://zoobank.org/DD01594B-5E3E-4F92-9877-96AF05CCDE2C

Ceriantheopsis lineata Stampar et al., 2015c: 1475–1481

Type locality. off Quequén, Buenos Aires, Argentina.

Distribution. Warm temperate south-western Atlantic, from Argentina (Buenos Aires State) to Brazil, Laje de Santos (São Paulo State), at 5–130 m depth.

Remarks. This species was recently described, and little is known beyond a detailed morphological description. Similar to *Ceriantheopsis austroafricanus*, this species shows considerable variation in color pattern (Stampar et al. 2015b). The deepest record of the species is 130 m from a dredging expedition (Stampar et al. 2015b). However, it is possible that the species occurs at even greater depths.

Type material. Museu de Zoologia da Universidade de São Paulo – MZUSP 2686 (Holotype).

7 *Ceriantheopsis nikitai* Molodtsova, 2001

http://zoobank.org/References/F11F4732-5C5A-4A8D-BDDE-13D8888B11DC

Ceriantheopsis nikitai Molodtsova, 2001a: 773–780; Stampar et al. 2015c: 1475, 1480

Type locality. Benguela Upwelling System, Namibia.

Distribution. Only known from deep water at the type locality (145–240 m depth).

Remarks. This species was recently described and has not been the subject of any study since the original description of the species by Molodtsova (2001a). Recorded only from a restricted area in Namibia, this species occurs sympatrically with two other species, *Botrucnidifer shtokmani* and *Cerianthus malakhovi*. These three species were found in the same upwelling system, which suggests that they can also occur in deeper areas.

Type material. Zoological Museum of Moscow University – ZMMU UE-97 (Holotype).

Genus *Cerianthus* Delle Chiaje, 1841

Table 3

Type species. *Cerianthus membranaceus* (Spallanzani, 1784)

Number of valid species: 18

8 *Cerianthus andamanensis* Alcock, 1893

http://zoobank.org/0767B24E-372F-4A41-B206-BE26CF12FE37

Cerianthus andamanensis Alcock, 1893: 153; Carlgren 1896: 174; Pax 1910: 167; Molodtsova 2001b: 913

(?) *Cerianthus andamanensis*: Haldar 1981: 60–61

Type locality. off Port Blair, Andaman and Nicobar Islands, India.

Distribution. Only known from shallow water at the type locality.

Remarks. The species description is based on three specimens from Port Blair in the Andaman Sea (Alcock 1893); it is very simple with scant information on anatomy. The only two useful pieces of published information are related to the size of the preserved specimens (up to 10 cm in length), and the number of marginal tentacles (up to 160). The specimens observed by Alcock (1893) should be placed within the family Cerianthidae, but currently it is not possible to state that this species is truly part of the genus *Cerianthus*, and a systematic examination of this species is needed. The material recorded by Haldar

Table 3. Comparison of anatomical features of *Cerianthus* species.

Species	Directive mesenteries length	Directive labial tentacle	M-mesentery (M1) length	M-mesentery (M2) length	M-mesentery (m1) length	M-mesentery (m2) length	Mesenteries attached to siphonoglyph	Siphonoglyph shape	Number of marginal tentacles
C. andamanensis	–	–	Reach aboral pore	–	–	–	–	–	~160
C. bathymetricus	–	–	Reach aboral pore	1/2 of M-1	–	–	–	Wide?	28
C. filiformis	> stomodeum	Present	Reach aboral pore	6/8 of M-1	7/8 of M-1	5/8 of M-1	6	Wide?	~70
C. incertus	–	–	–	–	–	–	–	–	38-42
C. japonicus	> stomodeum	Present	Almost reach aboral pore	≅ M-1	3/4 of M-1	~1/2 of M-1	4?	Wide	65
C. lloydii	> stomodeum	Present	Almost reach aboral pore	Longer than M-1	1/5 of M-1	1/6 of M-1	4	Narrow	Up to 70
C. malakhovi	?		Half column (?)	> M-1	?	?	?	?	~160
C. medusula	?	?	?	?	?	?	?	?	Few
C. membranaceus	> stomodeum	Present	Almost reach aboral pore	≅M-1	≅P2	≅m-1	6	Narrow	140
C. mortenseni	>stomodeum	Present	Short, almost half of gastrovascular cavity	≅ M-1	3/4 of M-1	1/2 of M-1	8	Wide	125
C. punctatus	> stomodeum	Present	Almost reach aboral pore	=M-1	2/3 of M-1	1/4 of M-1	6	Rather wide	80-90
C. roulei	?	?	Long?	?	?	?	?	?	~40
C. stimpsonii	?	?	?	?	?	?	?	?	?
C. sulcatus	> stomodeum	Present	Reach aboral pore	≅M-1	?	?	?	Narrow	~180
C. taedus	> stomodeum	Present	Short?	Short	?	?	?	Narrow	55
C. valdiviae	≅stomodeum	Absent	Short?	=M-1	≅M-1	1/2 of M-1	4	Narrow	35
C. vas	?	?	?	?	?	?	?	?	?
C. vogti	> stomodeum	Present	(?)Almost reach aboral pore	(?)Longer than M-1	(?)1/5 of M-1	(?)1/6 of M-1	?	Narrow	30-40

(1981) is probably not the same species since the biogeographical region is different, but owing to the absence of a detailed description no definite conclusions can be drawn.

Type material. (?) Indian Museum.

9 *Cerianthus bathymetricus* Moseley, 1877

http://zoobank.org/6078abf1-2d50-4e1f-b956-2cee43bb5f87

Cerianthus bathymetricus Moseley, 1877: 302–305; Andres 1883: 350; van Beneden 1897: 142; Pax 1910: 167; Mello-Leitão 1919: 37; Molodtsova 2000: 14–15, 17, 19; Molodtsova 2001b: 913

Type locality. Deep sea, North Atlantic (35° 26'N 50° 53'W), at 5000 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species is one of the smallest tube-dwelling anemone species known. The described specimens are only 2.5 cm long and lived in a very long membranous tube of more than 11 cm in length. The description is not detailed but provides some information on the anatomy, indicating a very long hyposulcus (especially in figure 17, Moseley 1877). Molodtsova (2001b) proposed that this species should be placed within the family Arachnactidae, however we are uncertain about this classification as some species of Cerianthidae have comparatively long hyposulcus regions, and the small size of this species may be misleading. Additionally, the description of the tube is much more consistent with the organization of Cerianthidae (see Stampar et al. 2015a). Thus, we choose to maintain this species as valid until additional studies say otherwise.

Type material. Not found in this study, but the original description provided a graphic representation.

10 *Cerianthus filiformis* Carlgren, 1924

http://zoobank.org/E466344E-55C1-4CE8-B84F-27BC677961F9

In part *Cerianthus orientalis* Verrill 1865: 151
Cerianthus sp. 1 Wassilieff 1908: 46
Cerianthus sp. 2 Wassilieff 1908: 46
Cerianthus filiformis Carlgren, 1924: 169–173; Uchida 1979: 195–197; Song 1986: 79–87; Song and Lee 1998: 239–240; Song 1998: 195–198; Pei 1998: 179–180; Song 2000: 324–326; Uchida and Soyama 2001: 127, 150, 152
Cerianthus misakiensis Nakamoto, 1923: 167

Type locality. Aburatsubo Bay, Miura, Japan.

Distribution. South Japan, South Korea, Korea (East China Sea), and China (Yellow Sea), at 1–50 m depth.

Remarks. There are some detailed descriptions about this species (e.g., Nakamoto 1923; Carlgren 1924). Uchida (1979) described the color variation of specimens from Japan (Kushimoto) and some ecological aspects. The same author also compared *C. filiformis* to other specimens described from the same area and concluded that all specimens belonged to the same species. This assumption includes the specimen from Okinose Bank, Sagami Bay (Kanagawa, Japan) described by Wassilieff as *C. orientalis* Verril, 1865. This specimen is deposited in the Zoologische Staatssammlung München (ZSM; 173/D65) and does not belong to the genus *Cerianthus* but to *Ceriantheomorphe* (S. Stampar pers. obs.). It is not very well preserved, but the overall organization of the mesenteries is quite consistent with that of *Ceriantheomorphe ambonensis* (Kwietniewski, 1898). The occurrence of *Ceriantheomorphe* in Japanese waters was also discussed by Molodtsova (2001b).

Type material. Lund Museum of Zoology – MZLU L930/3095b (Syntype).

11 *Cerianthus incertus* Carlgren, 1932

http://zoobank.org/8570871C-238B-47B6-A113-4FD870CEF0C5

Cerianthus danielsseni Levinsen, 1893: 398; Carlgren 1896: 174; Roule, 1904: 792; Kingsley 1904: 347; Roule 1905: 85–89; Pax 1910: 167; Carlgren 1912a: 5; Carlgren 1942: 71

Cerianthus incertus Carlgren, 1932: 255; Molodtsova 2000: 14–15; Molodtsova 2001b: 913; Molodtsova 2014: 100

Type locality. North Sea (not specified).

Distribution. Arctic Ocean, Norway, and Iceland, at 650–1185 m depth.

Remarks. *Cerianthus incertus* has a complicated taxonomic history and was originally described as *C. danielsseni* by Levinsen (1893) based only on its external morphology. Carlgren (1896) discussed this problem and, later, Roule (1905), based on specimens from nearby locations, described a new species using the same name. However, at this point, the name *C. danielsseni* became a homonym and was no longer available according to the rules of the International Commission on Zoological Nomenclature (ICZN). Thus, Carlgren (1932) suggested a new name (*Cerianthus incertus*) to solve both situations. Molodtsova (2014) postulated that *C. incertus* is a junior synonym of *C. vogti*, but there are no data available to confirm this hypothesis. Despite discussions on the past taxonomic confusion, this species is still understudied.

Type material. Not found in this study.

12 *Cerianthus japonicus* Carlgren, 1924

http://zoobank.org/116CDC46-02C7-4B61-B791-F1228F8AD3D3

Cerianthus japonicus Carlgren, 1924: 173–175, Uchida 1979: 185–194; Molodtsova 2000: 19; Molodtsova 2001b: 913

Type locality. Aburatsubo, Misaki (Sagami Bay), Japan.

Distribution. Sagami Bay and Miyazaki, Kyushu Island, Japan; North Hamgyong Province, North Korea, at 10–100 m depth.

Remarks. The original species description was based on two small specimens, one from North Korea (North Hamgyong Province) and the other one from Japan, Aburatsubo, Misaki (Sagami Bay). The description is quite adequate and presents the most important characteristics of the species. However, as noted by Molodtsova (2001b), differences between *C. japonicus* and *C. punctatus* Uchida, 1979 are very subtle. There are only two reliable characters that can be used to differentiate the two species: (1) the organization of the tentacular pseudocycles and (2) the number of mesenteries attached to the siphonoglyph. The first is a plastic character and intraspecific variation has been reported (Carlgren 1912a; Arai 1965), while the second seems to be consistent (Stampar et al. 2016). However, figure 4 by Carlgren (1924) does not allow verification if the third pair of mesenteries (P3) is in contact with the siphonoglyph or not. If the siphonoglyph format is the same as indicated by Uchida (1979), the P3 is probably also connected. Most data indicate that *C. punctatus* is synonymous to *C. japonicus*, which currently cannot be confirmed based on the available data.

Type material. Museum of Evolution- Evolutionsmuseet (Uppsala University – ZTY 2516) (Holotype).

13 *Cerianthus lloydii* Gosse, 1859

http://zoobank.org/F0DC99E3-1FB9-4729-9316-01535953DD3A

Edwardsia vestita Gosse, 1856a: 74–75

Cerianthus membranaceus Gosse, 1858: 419

Cerianthus lloydii Gosse, 1859: 50; Gosse 1860: 268–274; Fischer 1874: 201; M'Intosh 1875: 38–39; Robertson 1876: 25, 30; Koren and Danielssen 1877: 80; Andres 1883: 554; Hartlaub 1884: 203; Fischer 1887: 383–384, 432, 437; Carlgren 1893: 120–123, 133, 148; van Beneden 1897: 139–140, 142; Fowler 1897: 806; Haddon 1898: 401; Gravier 1902: 592; Gravier 1904: 259, 267, 276, 278, 280, 288; Roule 1904: 791–792; Roule 1905: 83–85; Walton 1908: 215, 225–226; Torrey and Kleeberger 1909: 117; Pax 1910: 166; McMurrich 1910: 10–11, 17–18; Carlgren 1912a: 11–18; Mello-Leitão 1919: 36, 39; Gravier 1922: 88–89; van Beneden 1924: 101–116, 126, 154; Pax 1928: 201, 234; Stephenson 1928: 83–84; Carlgren 1928: 255–263; Carlgren 1931: 10; Leloup 1931: 2, 3, 5–9; Carlgren 1932: 264–266; Müllegger 1938: 2, 12, 13; Carlgren 1940: 9, 10; Carlgren 1942: 69–71; Nyholm 1943: 95–140, 193–227; Dons 1945: 20; Carlgren 1945: 67–69, 71, 155; Teissier 1950: 33; Williams 1954: 52; Füller 1957: 31; Robins 1969: 339; Riemann-Zürneck 1969: 170, 199, 201, 210, 211, 225; Cutress 1961: 80; Laverack and Blackler 1974: 28; Manuel 1977: 484; den Hartog 1977: 233; Uchida 1979: 194; Manuel 1981: 64–66; Ates 1982: 80–83; Braber and Borghouts 1977: 16, 17; Eleftheriou and Basford 1983: 147–157; Ates 1985:

230–232; Chintiroglou and Koukouras 1991: 395; Harms 1993: 16; Molodtsova and Malakhov 1995a: 5–16; Molodtsova and Malakhov 1995b: 4–11; Ates 1997: 10, 18, 24, 25; Sebens 1998: 48; Blanco 1987: 198; Vafidis and Koukouras 1998: 123; Moore and Cameron 1999: 369–370; Molodtsova 2000: 3, 7, 12–13, 17; Molodtsova 2001a: 778; Molodtsova 2001b: 919; Molodtsova 2001c: 1035; Grebel'nyi 2001: 36; Uchida and Soyama 2001: 129, 150, 152; Molodtsova 2001d: 9, 10; Molodtsova 2003: 252; Molodtsova 2004a: 297; Molodtsova 2004b: 261; Wieking and Kröncke 2005: 395–396; Brown and Collier 2007: 207; Rehm and Rachor 2007: 130, 132; Schückel et al. 2010: 5–7, 9; Bolam et al. 2011: 2239, 2241; Strain et al. 2012: 63–65; Sciberras et al. 2013: 91, 93, 95; Peckett et al. 2014: 336; Coolen et al. 2015: 87

(?) *Cerianthus borealis* Danielssen, 1860: 251; Verrill 1873b: 405, 414; Danielssen 1888: 1–12; van Beneden 1924: 91, 120–127, 128–131

Cerianthus vermicularis Lütken, 1860: 199–200

Cerianthus lutkenii Andres, 1883: 353

Arachnactis bournei Fowler, 1897: 805–807 (larval stage)

Cereanthus lloydii Goette, 1897: 293

Cerianthus lloydii borealis Grieg, 1913: 142

Synarachnactis bournei Leloup, 1962: 2–4, 6–7 (larval stage)

Cerianthus septentrionalis van Beneden, 1924: 120: 126–131; Molodtsova 2001d: 9–10

(?) *Cerianthus* sp. Tarasov et al. 1990: 1–3; 6; 15, 17

(?) *Cerianthus lloydii*: Kussakin and Kostina 1996: 207; Çinar et al. 2014: 684

Type locality. Menai Strait, Irish Sea, United Kingdom.

Distribution. North Sea, Norwegian Sea, Barents Sea, Greenland Sea, Bay of Biscay, and (?) Sea of Okhotsk; (?) depths from 2 m to the deep sea,

Remarks. This species has been the subject of many studies. There have been several morphological descriptions (e.g., Gosse 1860; Carlgren 1912a; Molodtsova and Malakhov 1995a) and several aspects of its ecology and life cycle have been investigated (e.g., van Beneden 1924; Nyholm 1943; Molodtsova and Malakhov 1995b). However, two points still need further attention. The first is related to the distribution of the species, as the presence of some disjointed records in the Pacific Ocean raise the possibility of a disjunct distribution (e.g., more than one species contained in these records). However, the presence of larvae in plankton for long periods of time (Nyholm 1943) may explain the very large occurrence areas as already known for other Ceriantharia species (Stampar et al. 2015c). Braber and Borghouts (1977) reported the occurrence of this species from an estuary system (salinity around 16 psu), and Çinar et al. (2014) from the coast of Turkey, although the second record is questionable. The second point is related to the position of the species within the genus *Cerianthus*. Preliminary studies (unpublished) based on molecular data indicate that perhaps this species is more related to the genus *Cerianthopsis* than to *Cerianthus*.

Type material. Not found in this study.

14 *Cerianthus malakhovi* Molodtsova, 2001

http://zoobank.org/830A9DD9-8EE9-4849-94EA-D89979D06926

Cerianthus malakhovi Molodtsova, 2001a: 909–913; Molodtsova 2001b: 913; Molodstova et al. 2011: 1

Type locality. Close to Torra Bay and Mowe Bay, Skeleton Coast Park, Namibia; at 300–350 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species has been described in detail relatively recently based on five collected specimens. The original description, in Russian, contains no information on living animals because the material examined was already fixed at the time of diagnosis. This is a species that requires attention, as it can occur in deeper waters and may contain very important evolutionary information.

Type material. Zoological Museum of Moscow University, ZMMU EC-102 (Holotype).

15 *Cerianthus medusula* (Klunzinger, 1877)

http://zoobank.org/0D8AA956-7C46-4DCA-889E-32BCFC84F419

Paractis medusula Klunzinger, 1877: 71–72

Cerianthus medusula Andres, 1883: 353–354; Cerfontaine 1891a: 37–38; van Beneden 1897: 141; Mello-Leitão 1919: 36

(?) *Pachycerianthus maua*: Krempf 1905: 195

(?) *Pachycerianthus mana*: Fishelson 1970: 109

Type locality. Al-Qusair (Red Sea), Egypt.

Distribution. Only known from shallow water (at < 5 m depth) at the type locality.

Remarks. This is another species with only little available data, and these are quite contradictory. This species was described as a sea anemone (order Actiniaria) by Klunzinger (1877) based only on the external morphology. Andres (1883) described some aspects of the external morphology based on work by Klunzinger (1877) and indicated that this must be a species of family Cerianthidae. Cerfontaine (1891a) argued that this species may be the same as *C. oligopodus* (= *Arachanthus oligopodus*) found in Italy, and furthermore the specimen observed by Klunzinger (1877) was not in good condition. However, it is not possible to make more statements about this species due to the absence of material available from the region. On the other hand, the indication that this species is a member of the family Arachnactidae as stated by Cerfontaine (1891a) seems to be incorrect. The few characters present in the descriptions are not consistent with those of the Arachnactidae, but instead with those of the Cerianthidae. This is a species that requires additional sampling from the type locality for further examination, especially as some specimens identified as *Pachycerianthus maua* Carlgren, 1900 have been subsequently collected from the same region (Krempf 1905; Fishelson 1970).

Type material. Not found in this study, but the original description provided a graphic representation.

16 *Cerianthus membranaceus* (Gmelin, 1791)
http://zoobank.org/3AD7FFEB-56C0-49A3-9BDB-00A813327D90

Tubularie Spallanzani, 1784: 627–628
(?) *Tubularie*: Rapp 1829: 656–658
Tubularia membranosa Gmelin, 1791: 3836
Actinia cylindrica Renier, 1807: 23
Actinia vestita Renier, 1807: 23–24
Moschata rhododactyla Renier in de Blainville, 1830: 284; de Blainville 1834: 318;
Cereus cupreus Ilmoni, 1830: 698–699; Ilmoni 1831: 123
In part *Actinia elongata* Grube, 1840: 11–12; Sars 1857: 33
Cerianthus cornucopia Delle Chiaje, 1841: 136; Milne Edwards and Haime 1851: 14
Cerianthus breae Delle Chiaje, 1841: 136
Cerianthus actiniodeus Delle Chiaje, 1841: 136
Cerianthus membranaceus: Haime 1854: 352–389; Milne-Edwards 1857: 309; Sars 1857: 28–32; Agassiz 1863: 529; Fischer 1874: 200–203, 237–239; Fischer 1875: 184–185; Heider 1879: 204–254; Jourdan 1880: 16, 44–45, 103–117, 130–132, 152–153; Andres 1881: 331–332; Andres 1883: 347–349; Mark 1884: 42; Graeffe 1884: 340; Fischer 1887: 383–385, 405, 432, 435; Hertwig 1888: 54; Fischer 1889 252, 254–265; Hickson 1889: 8; Cerfontaine 1891a: 37; Cerfontaine 1891b: 133–141; Goette 1897: 292–316; van Beneden 1897: 54–56, 139, 142; Gravier 1902: 592; Child 1903a: 239–260; Child 1903b: 10; Child 1904a: 70–71; Child 1904b: 279–284; Gravier 1904: 259, 269, 276, 278, 280; Carlgren 1906: 77–78; van Beneden 1924: 18, 28, 59, 30–68, 70, 73, 77, 85, 92, 94, 104, 108, 135–144, 163–164, 175; Carlgren 1927: 443; Menon 1927: 31–32; Torelli 1932: 2–15; Müllegger 1938: 2, 12; Pax and Müller 1955:110; Leloup 1960:1–3; Pax and Müller 1962: 107–110; Leloup 1962: 3–4, 6–7; Schmidt 1972: 427, 429, 431, 433; Schmidt 1974: 535, 537, 547; den Hartog 1977: 233, 235; Uchida 1979: 194; Ates 1982: 80–83; Tur and Godall 1982: 178, 180–182; Gili 1982: 120, 125–126; Ates 1985: 230; Morri et al. 1991: 37; Chintiroglou et al. 1995: 362; Vafidis and Koukouras 1998: 119–120, 123; Molodtsova 2000: 14, 17; Ocaña et al. 2000a: 57; Molodtsova 2001b: 913; Molodtsova 2004: 261; Wiedenmann et al. 2004: 270, 272–274, 276; Calado 2006: 391; Nienhaus et al. 2006: 12942–12943; Casellato et al. 2007: 127, 129; Cosentino et al. 2011: 409–411, 413–414; Lo Iacono et al. 2012: 466–467; Rastorgueff et al. 2015: 142, 148; Stampar et al. 2015b: 2167
(?) *Edwardsia vestita* Gosse, 1856a: 74–75; Gosse 1856b: 220; Milne-Edwards 1857: 286; Gray 1867: 240
(?) *Cerianthus membranaceus*: Gosse 1858: 419; Heller 1868: 20, 79
Cerianthus cylindricus Milne-Edwards, 1857: 309; Heller 1868: 20, 79
Saccanthus purpurescens Milne-Edwards, 1857: 310

Cerianthis membranaceus: Sars 1857: 28–32
(?) *Cerianthus lloydii* Gosse, 1859: 419; Çinar et al. 2014: 684
Cerianthus membranaceus nigricans Andres, 1881: 332
Cerianthus membranaceus violaceus Andres, 1881: 332
Cerianthus membranaceus viridis Andres, 1881: 332
Cerianthus membranaceus roseus Andres, 1881: 332
Cerianthus nans Andres, 1881: 333
Saccanthus purpurascens Andres, 1883: 351
Saccanthus purpurensis van Beneden, 1897: 142
Pachycerianthus multiplicatus: Çinar et al. 2014: 684

Type locality. Mediterranean Sea, Italy (not specified).

Distribution. Mediterranean Sea (Italian coast), shallow waters.

Remarks. This is one of the most well-known cerianthid species, but at the same time there are many questions about the taxonomic consistency of past works. This was the first species of Ceriantharia described (type locality Italy); however, this has caused many records from the Mediterranean Sea being incorrectly attributed to this species. For example, Pax (1908) argued that *C.* (*Saccanthus*) *maderensis* (= *Isarachnanthus maderensis*) Johnson, 1861 is synonym of *C. membranaceus* based on the two species' original descriptions. However, the descriptions presented and discussed by Johnson (1861) and Pax (1908) are incompatible with *C. membranaceus* and more likely describe a species of the family Arachnactidae, perhaps a member of the genus *Isarachnanthus*. In addition, *I. maderensis* is very common in Madeira and the Azores (Stampar et al. 2012; Stampar and Morandini 2017). Haque (1977) recorded *C. membranaceus* from Bangladesh and Pakistan, but these records are biogeographically incongruent and probably these specimens from the Indian Ocean are another species. In short, *C. membranaceus* is a species that requires a comprehensive review of all its records, especially for the presence of cryptic species, and to assess if the different morphotypes reported truly belong to just one species or to a species complex.

Type material. Not found in this study.

17 (?) *Cerianthus mortenseni* Carlgren, 1924

http://zoobank.org/3AA339E2-4BFC-424A-997A-BBEA7EB45041

Cerianthus mortenseni Carlgren, 1924: 175–182, 195; Molodtsova 2001b: 773

Type locality. Paniquian Island, Mindoro, Philippines.

Distribution. Only known from shallow water at the type locality.

Remarks. This is a very intriguing species as the two specimens described in the original description are very different in shape. The organization of the mesenteries is not coincident on both sides of the body, indicating a considerable difference in the development of mesenteries (Carlgren 1924). This sort of large variation is not commonly reported in tube-dwelling anemones. The mesentery organization and associated structures indicate

a strong correlation of these specimens with the genera *Cerianthus* and *Pachycerianthus*. Thus, this species may be important in the ongoing discussion about the validity of the genus *Pachycerianthus* (Torelli, 1961). Unfortunately, these are the only two specimens collected from the type locality (Philippines). Other specimens examined from this area (S. Stampar pers. obs.) are not similar to the specimens described by Carlgren (1924).

Type material. Department of Zoology, University of Stockholm, Sweden (holotype) (?).

18 *Cerianthus punctatus* Uchida, 1979

http://zoobank.org/DBEE9A26-932A-4F64-B0D5-12BF79BA5E33

Cerianthus punctatus Uchida, 1979: 189–195; Molodtsova 2000: 19; Uchida and Soyama 2001: 129, 150, 152; Molodtsova 2001b: 913

Type locality. Suruga Bay (Numazu), Japan.

Distribution. Only known from shallow water at the type locality.

Remarks. The available information on this species is amongst the most complete from before the advent of detailed descriptions in the 2000s. Uchida (1979) gives a complete comparison of several characters with most species of the genus *Cerianthus*. However, besides morphological data there is still no other information about this species (e.g., reproduction).

Type material. Saibura Marine Park Research Station (lost?), but the original description provided a graphic representation.

19 *Cerianthus roulei* Carlgren, 1912

http://zoobank.org/8180341D-C667-45AF-9A80-B85DB5C6B2CD

Cerianthus lloydii Gosse, 1859: 50; Roule 1904: 791–792; Roule 1905: 83–85; van Beneden 1924: 111–116

Cerianthus roulei Carlgren, 1912a: 3–5; Carlgren 1932: 255–256; Carlgren 1942: 71; Molodtsova 2001b: 913

Type locality. close to Svalbard, Norway, Greenland Sea.

Distribution. Svalbard, Norway, Greenland Sea; depth unknown.

Remarks. This species has a very deficient description and is represented by very few museum specimens for comparison. The description of *C. lloydii* by Roule (1905) (see synonymy list) may fit a range of species (e.g., *Cerianthus lloydii*, *Ceriantheopsis americana*) and thus it is not possible to discuss it based on these data. The type locality is difficult to reach, and it may be very problematic to obtain additional specimens due to the absence of precise locality data and because material is likely to be from great depths up to 5000 m (Ritzmann et al. 2004). Therefore, the validity of this species remains uncertain.

Type material. Not found in this study.

20 (?) *Cerianthus stimpsonii* Verrill, 1868

http://zoobank.org/555D3481-FEF5-4615-9C3F-DE58BB8B4EE8

Cerianthus stimpsonii Verrill, 1868: 317–318; Verrill 1870: 102; Andres 1883: 351–352; van Beneden 1897: 140; Pax 1910: 167; Mello-Leitão 1919: 36; Molodtsova 2001b: 913

Type locality. Port Lloyd, Bonin Islands (Ogasawara Islands), Japan.

Distribution. Only known from shallow water (18 m depth) at the type locality.

Remarks. Based on the description by Verrill (1868), this species probably belongs to the family Arachnactidae, particularly due to the description of a soft tube (see Stampar et al. 2015b). The few external characters presented are only consistent with those of the family Arachnactidae. Unfortunately, there are no specimens from the Ogasawara Islands deposited in museums, and further discussions on this point depends on finding some material that can be correlated with the type material or else new collections for the designation of a neotype.

Type material. Not found in this study.

21 *Cerianthus sulcatus* Kwietniewski, 1898

http://zoobank.org/98D51C07-651B-4476-8409-BE60BA39C86A

Cerianthus sulcatus Kwietniewski, 1898: 427; Pax 1910: 167; Carlgren 1912a: 44–47; Uchida 1979: 194; Molodtsova 2001b: 919

(?) *Cerianthus sulcatus*: McMurrich 1910: 28–30

Type locality. Raha, Ambon, Moluccas, Indonesia.

Distribution. Only known from shallow water at the type locality.

Remarks. This species was described by Kwietniewski (1898) based on a 4 cm long and 2.5 cm wide specimen with 90 tentacles in each tentacle series (marginal and labial) and three cycles each. However, these are the only characteristics indicated. McMurrich (1910a) gave a description of a specimen collected from near the type locality. However, the description is incomplete and presents some differences compared to original description. Thus, currently, we cannot confirm if this species is valid or not.

Type material. Not found in this study.

22 *Cerianthus taedus* McMurrich, 1910

http://zoobank.org/DBA7107E-9E29-43D3-8345-822BB1D77067

Cerianthus taedus McMurrich, 1910: 30–31; Carlgren 1912a: 44–47; van Soest 1979: 117; Pei 1998: 181

Type locality. Makassar Strait, Central Sulawesi, Indonesia.

Distribution. Only known from deep water (at 724 m depth) at the type locality.

Remarks. This species was described based on only one damaged specimen, which was 6 cm long, with 55 marginal and labial tentacles arranged in two and four cycles, respectively. The organization of the mesenteries was not described in detail by McMurrich (1910), who simply indicated the alternation of fertile and sterile mesenteries. There are several observations of different morphotypes that are not formally associated with any other name described from this or related areas. As there are no other species described for this region with this morphotype, it is probably a valid species, but it is not possible to certainly state that this species belongs to *Cerianthus*.

Type material. Possibly lost (Zoological Museum of Amsterdam, now Naturalis Biodiversity Center, Leiden).

23 *Cerianthus valdiviae* Carlgren, 1912

http://zoobank.org/15818B70-049E-4801-AFB0-A1D1E69FCA4A

Cerianthus valdiviae Carlgren, 1912a: 44–47; Carlgren 1923: 245–252; Uchida 1979: 193; Molodtsova 2001b: 929

Type locality. Between Keeling and south Sumatra, Indian Ocean.

Distribution. Only known from deep water (at 5000 m depth) at the type locality.

Remarks. This species was initially described in a table by Carlgren (1912a). However, the same author redescribed this species in 1923 in more detail. This is a species from the deep sea; however, the detailed description allows confirmation that this species belongs to *Cerianthus*. This is another example of a species that needs further study, as it may present very different characters compared to species from shallow waters.

Type material. Not found in this study.

24 *Cerianthus vas* McMurrich, 1893

http://zoobank.org/c01102cc-ec9d-474a-968e-82b0bbe5686f

Cerianthus vas McMurrich, 1893: 202–203, 206; Carlgren 1896:174; Haddon 1898: 401; Torrey and Kleeberger 1909: 115 -116; Pax 1910: 167; Arai 1965: 205

Type locality. Cedros Island, Mexico (Pacific coast).

Distribution. Only known from shallow to deep water (at 80 m depth) at the type locality.

Remarks. This is a doubtful species, as the original description is very incomplete, and some characters are incongruent. Torrey and Kleeberger (1909) comment that *Cerianthus vas* is a very problematic species, but they did not discuss the problems in detail. This species may actually be valid, but due to the absence of materials from the same depth and location, it is not possible to further discuss this.

Type material. Not found in this study, but the original description provided a graphic representation.

25 *Cerianthus vogti* Danielssen, 1890

http://zoobank.org/3B09DBC0-6D5E-4371-AAD7-94F8DAA4DABC

Cerianthus vogti Danielssen, 1890: 137–142; Carlgren 1895: 284; Roule 1905: 89; Pax 1910: 167; Carlgren 1912a: 18–21; Mello-Leitão 1919: 36–38; Carlgren 1932: 255; Carlgren 1942: 69, 71; Jensen 1992: 75–80; Molodtsova 2000: 15,17; Molodtsova 2001b: 919

Cerianthus abyssorum Danielssen, 1890: 143; Carlgren 1895: 284; van Beneden 1897: 140; Roule 1905: 89; Pax 1910: 167; Mello-Leitão 1919: 36

Type locality. Norwegian Sea (not specified).

Distribution. Only known from deep water (at 900–1400 m depth) at the type locality.

Remarks. This species is well known, even though it is a species from deeper areas. The description by Danielssen (1890) is incomplete as it presents few characters related to the organization of the mesenteries. Nevertheless, it is quite detailed in various other aspects. Carlgren (1912a) presents a slightly more complete description with more comprehensive information on the organization of the mesenteries and a comparison with *C. lloydii*. Jensen (1992) presents environmental and biological data about the species, especially on the occurrence of branching and fairly long tubes (tube system).

Type material. Not found in this study.

Genus *Pachycerianthus* Roule, 1904

Table 4

Type species. *Pachycerianthus multiplicatus* Carlgren, 1912a (proposed by Kelly and Keegan 2000)

Number of valid species: 16

26 *Pachycerianthus aestuarii* (Torrey & Kleeburger, 1909)

http://zoobank.org/3DEBCB69-32C3-4CDD-8F03-AFBD67DFDBB8

Cerianthus aestuarii: Child, 1908: 27–53; Torrey and Kleeburger 1909: 115–119, 121, 123; Pax 1910: 167; Pei 1998: 181

Pachycerianthus aestuari: McMurrich, 1910: 11; Arai 1965: 205, 210; Arai 1971: 1680; Carter 1995: 6

Pachycerianthus aestuarii: Carlgren 1912a: 44–47; Stampar et al. 2014b: 345, 350, 352

Type locality. Mission Bay, East Pacific, California, United States of America.

Distribution. East Pacific, California, USA, shallow waters.

Remarks. This species was described by Torrey and Kleeburger (1909) based on specimens obtained from Mission Bay, California. This description is not very detailed but relevant information about its morphology is available. Child (1908) described some information on the movements and regeneration of *P.* (*Cerianthus*) *aestuarii* and morphological adaptations in relation to the environment. Carlgren (1912a) moved the species to genus *Pachycerianthus* based on the original description. Arai (1965) described a new species of the same genus, *P. torreyi*, from a nearby area and claimed that this was not the same species as described by Torrey and Kleeburger (1909). This species was considered a synonym of *P. fimbriatus* by Arai (1971), which occurs in the same area as *P. aestuarii*.

Type material. Not found in this study, but the original description provided a graphic representation.

27 *Pachycerianthus borealis* (Verrill, 1873)

http://zoobank.org/73181FBE-06D8-416C-8C79-C94AF7FB94E7

Cerianthus borealis: Danielssen 1860: 251 (senior homonym); Verrill 1873b: 5,14; Verrill 1873a: 349, 350, 368, 391; Verrill 1873c: 440–441; Verrill 1874: 413; Harger and Smith 1876: 54; Verrill 1879: 15; Andres 1883: 352; Verrill 1885: 534; Danielssen 1888 1–12; McMurrich 1893: 204; van Beneden 1897: 140 -142; Parker 1900: 757; Kingsley 1904: 345–359; Torrey and Kleeburger 1909: 119, 125; McMurrich 1910a: 167; Pax 1910: 167; Carlgren 1912a: 44–47; Mello-Leitão 1919: 36; 37; Verrill 1922: 134–136; van Beneden 1924: 91, 120–127, 128–131; MacGinitie 1955: 61, 75, 84, 85, 97, 122; Widersten 1976: 857, 858; Shepard et al. 1986: 625–646; Sebens 1998: 13, *16, 21, 57; Molodts*ova 2001d: 9; Molodtsova 2004b: 261

Cerianthus verrillii McMurrich, 1910: 10–11

Pachycerianthus borealis: Molodtsova 2000: 15, 17; Molodtsova 2001b: 9; Stampar et al. 2014b: 344–345, 350, 352–353

Type locality. Georges Bank, Massachusetts, United States/Nova Scotia, Canada (not specified).

Distribution. Northwestern Atlantic (Arctic Sea to North Carolina, USA), at depths of 10–500 m.

Remarks. This species was described by Verrill (1873b) based on external morphology but he did not give many details. Danielssen (1888) gave a very detailed description, including various characters concerning the internal anatomy. A century later, Shepard et al. (1986) presented a study on ecological aspects of tube-dwelling anemones from the Northwest Atlantic and included some information about *Pachycerianthus* (*Cerianthus*) *borealis*. Molodtsova (2001b), in her discussion of the genus *Cerianthus*, showed that *Cerianthus borealis* should be part of the genus *Pachycerianthus*. This species occurs at lower temperatures and apparently resists considerable variations in salinity (S. Stampar pers. obs.).

Table 4. Comparison of anatomical features of *Pachycerianthus* species (after Stampar et al. 2015).

Species	Directive mesenteries length	Directive labial tentacle	M-mesentery (M1) length	M-mesentery (M2) length	M-mesentery (m1) length	M-mesentery (m2) length	Mesenteries attached to siphonoglyph	Siphonoglyph shape	Number of marginal tentacles
P. aestuari	> stomodeum	?	Reach aboral pore	≅ M-1	1/5 of M-1	= m-1	16	Wide	30–34
P. benedeni	< stomodeum	?	Reach aboral pore	?	?	?	6?	Wide?	~125
P. borealis	> stomodeum	?	Reach aboral pore	= M-1	3/4 of M-1	~1/3 of M-1	8	Wide	139–155
P. curacaoensis	> stomodeum	Absent	Reach aboral pore	1/2 of M-1	1/4 of M-1	2/3 of m-1	4	Short and narrow	74–105
P. delwynae	> stomodeum	Present	Almost reach aboral pore	Larger than M-1	1/3 of M-1	1/2 of M-1	6	Narrow	89–114
P. dohrni	?		Half column (?)	> M-1	?	?	?	?	~160
P. fimbriatus	> stomodeum	Present	Reach aboral pore	3/4 of M-1	1/3 of M-1	1/3 of M-1	8	Wide and long	<60
P. insignis	< stomodeum	Present	Almost reach aboral pore	≅M-1	≅M-1	≅M-2	8	?	~100
P. johnsoni	< stomodeum	?	Reach aboral pore	≅3/4 of M-1	3/4 of M-1	1/2 of M-1	8	Wide	~108
P. longistriatus	> stomodeum	Present	Reach aboral pore	=M-1	1/3 of M-1	1/4 of M-1	6	Wide	138–140
P. magnus	> stomodeum	Present	Almost reach aboral pore	3/4 of M-1	1/3 of M-1	1/2 of M-1	6	Short and narrow	~120
P. maua	< stomodeum	Absent	Reach aboral pore	1/4 of M-1?	1/3 of M-1?	1/3 of M-1?	6	Narrow	~150
P. monostichus	> stomodeum	Present	Reach aboral pore	≅M-1	1/2 of M-1	≅m-1	8	Narrow and long	~47
P. multiplicatus	> stomodeum	Absent	Reach aboral pore	=M-1	1/3 of M-1	1/3 of M-1	6	Narrow	175
P. nobilis	?	?	?	?	?	?	?	?	160–170
P. schlenzae	> stomodeum	Present	Reach aboral pore	3/4 of M-1	1/2 of M-1	1/3 of M-1	6	Long and narrow	60–85
P. solitarius	> stomodeum	Present	Reach aboral pore	≅ M-1	1/4 of M-1	1/5 of M-1	6	Narrow	~64

Type material. Peabody Museum of Natural History (Yale – YPM 9830, 9831, 9832 (Syntype).

28 *Pachycerianthus curacaoensis* den Hartog, 1977

http://zoobank.org/9599F783-723C-4B15-9949-3C80F5AB8B98

Pachycerianthus curacaoensis den Hartog, 1977: 215–221, 237; Carter 1995: 6; Molodtsova 2000: 15, 17; Stampar et al. 2014b: 344, 345, 350, 353

Type locality. Curaçao, Dutch Caribbean.

Distribution. Caribbean Sea (Curaçao), at 65–75 m depth.

Remarks. This species was described by den Hartog (1977) based on specimens from Curaçao. The description of this species is fairly detailed and includes a wide range of biological and morphological information. This is the only species of this genus in the Caribbean Sea and it shows no morphological similarity to congeners described from the Pacific Ocean. On the other hand, this species shares some characters with *P. schlenzae,* which was described from the South Atlantic (Stampar et al. 2014b). Thus, the evolutionary correlation of these two species is of biogeographical relevance.

Type material. Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie, Leiden – RMNH.COEL.11359 (holotype).

29 *Pachycerianthus delwynae* Carter, 1995

http://zoobank.org/96DDF06E-467C-47ED-9DB1-96E8085BC67A

Pachycerianthus delwynae Carter, 1995: 2–3; Molodtsova 2007: 133; Stampar et al. 2014b: 350, 352

Type locality. off Port Jackson, Sydney harbor, Australia.

Distribution. Sydney harbor, Australia, at 5–15 m depth.

Remarks. This is one of two species of this genus described from Australia by Carter (1995), the other one being *P. longistriathus*. They co-occur in the same bay and therefore doubts about the consistency of the two taxonomic species still exist. The morphological differences between the two species appear consistent, but intraspecific variation is quite significant and thus a more thorough evaluation of the morphological characters and the inclusion of molecular data may change this view.

Type material. Australian Museum; AMG15399 (holotype).

30 *Pachycerianthus dohrni* (van Beneden, 1924)

http://zoobank.org/3C1075B6-988C-4FB5-8855-FD4CC5DCA9D0

Cerianthus membranaceus viridis Andres, 1881: 332

Cerianthus membranaceus Andres, 1883: 347–349
Cerianthus dohrni: Lo Bianco 1909: 552; Pax 1910: 166; van Beneden 1924: 24, 30, 32, 33, 45, 60, 63, 65–89, 92, 94
In part *Cerianthus viridis* Torelli, 1932: 1–15
Pachycerianthus dohrni: Carlgren 1940: 15; Arai 1971: 1679; Carter 1995: 6; Vafidis and Koukouras 1998: 122–123; Stampar et al. 2014b: 350, 352

Type locality. Naples, Tyrrhenian Sea, Italy.

Distribution. Tyrrhenian Sea, Italy and Aegean Sea, Greece, shallow waters.

Remarks. This species was initially described from the Italian coast (Naples region) as a variation of *Cerianthus membranaceus* (Andres 1881). However, Lo Bianco (1909) recognized distinct differences from the material identified as *C. membranaceus* and suggested a new name, *Cerianthus dohrni*, but without giving a description. Subsequently, van Beneden (1924) gave a very detailed morphological description of the species with some observations from specimens in aquaria. Some years later, Torelli (1932) described *Cerianthus viridis* based on specimens with a morphology clearly related to that of *Cerianthus dohrni*. Carlgren (1940) relocated *C. dohrni* to the genus *Pachycerianthus*. This is one of the largest species of tube-dwelling anemones in the world with a length of more than 40 cm, which is comparable to the lengths of *Ceriantheomorphe brasiliensis* and *Cerianthus membranaceus*.

Type material. Not designated (several specimens mentioned, which can be considered syntypes).

31 *Pachycerianthus fimbriatus* McMurrich, 1910

http://zoobank.org/A1F21314-9AFC-42C8-A5DE-1A70BB00D3AE

(?) *Cerianthus elongatus* Kwietniewski, 1898: 426–427; Pax 1910: 167
Pachycerianthus fimbriatus McMurrich, 1910: 35–38; Carlgren 1912a: 44–47; Arai 1971: 1677–1680; Arai 1972: 311–317; Arai and Walder 1973: 1086–1088, 1090; Arai and Karakashian 1973: 719–720, 723–724; Tiffon and Hugon 1977: 289–290; Uchida 1979: 188; Carter 1995: 6; Fautin 1998: 135; Arai 1985: 47–48; Pirtle et al. 2012: 1896, 1905–1906; Stampar et al. 2014b: 350, 352
Pachycerianthus plicatus Carlgren, 1924: 182–186, 195; den Hartog 1997: 352; Arai 1971: 1677; 1680
(?) *Pachycerianthus torreyi* Arai, 1965: 205–210; Arai 1971: 1677; 1680

Type locality. Cebu, Philippines.

Distribution. Sulu Sea and Celebes Sea, Philippines, and Indonesia, (?) Pacific Coast of US and Canada; shallow waters.

Remarks. This species forms part of a taxonomic problem. The description of *P. fimbriatus* was based on a study of 15 specimens collected mainly from the Celebes Sea, Philippines, by McMurrich (1910). In the same study, McMurrich argued that

Cerianthus elongatus was the same as the new species *P. fimbriatus*, and considered Kwietniewski's (1898) description as incomplete and invalid. McMurrich (1910) also argued that *Cerianthus nobilis* described by Haddon and Shackleton (1893), based on specimens from North Australia, could also be the same species, but specimens were not available for comparison. Later, Arai (1965) described a new species from the Pacific Coast of North America, *P. torreyi*. The same author in 1971 recognized that this species was highly correlated with McMurrich's *P. fimbriatus* from the Celebes Sea. Thus, Arai (1971) considered *P. torreyi* to be a junior synonym of *P. fimbriatus*. However, the geographical distribution is disjunct by 14,000 km, and it is likely that a more detailed study with the inclusion of molecular data will present different results. In our opinion, *P. torreyi* should be a valid species.

Type material. The provenance data of a specimen in the Natural History Museum at London, NHMUK 1889.11.25.64, is coherent with the locality and dates in the original description, but it is impossible to make an exact connection between the materials.

32 *Pachycerianthus insignis* Carlgren, 1951

http://zoobank.org/046E54F7-B238-4BD9-8E51-0EFA1FD54917

Pachycerianthus insignis Carlgren, 1951: 435–436; Arai 1965: 205, 210; Arai 1971: 1679; Carter 1995: 6; Stampar et al. 2014b: 350, 352

Type locality. El Mogote, Baja California, Mexico.

Distribution. Gulf of California, Mexico; shallow waters.

Remarks. Although this species occurs in an area with a long history of marine research, it is still little known, and the only study focused on this species is the original description by Carlgren (1951). The species description is based only on one individual and therefore knowledge is quite limited and morphological variation is not known to date. Thus, this species still lacks taxonomic confirmation as well as other studies.

Type material. Smithsonian National Museum of Natural History – USNM 49454 (Holotype).

33 *Pachycerianthus johnsoni* (Torrey & Kleeburger, 1909)

http://zoobank.org/789ED1B7-5FEF-49D4-937E-4B20740A295E

Cerianthus johnsoni Torrey and Kleeburger, 1909: 116, 119, 123–125; Pax 1910: 167; Pei 1998: 181

Pachycerianthus johnsoni: McMurrich 1910: 11; Carlgren 1912a: 44–47; Arai 1965: 205, 210; Arai 1971: 1679; 1680; Carter 1995: 6; Stampar et al. 2014b: 350, 352

Type locality. Los Angeles, East Pacific, United States of America.

Distribution. Only known from shallow water at the type locality.

Remarks. This is another species described from the United States' Pacific Coast by Torrey and Kleeburger (1909) with a relatively good amount of detail; like *P. insignis*, there have been no more subsequent detailed or comparative studies. Arai (1971) has been the only author that has mentioned the morphological characters of this species after the original description, but even this characterization was based on the characters listed in the original description. The taxonomic status of this species is doubtful.

Type material. Not found in this study, but the original description provided a graphic representation.

34 *Pachycerianthus longistriatus* Carter, 1995

http://zoobank.org/96D33C91-AA78-42A2-918D-C9CB9B6B3EB8

Pachycerianthus longistriatus Carter, 1995: 3–5; Stampar et al. 2014b: 350, 352

Type locality. off Port Jackson, Sydney harbor, Australia.

Distribution. Sydney Harbor, Australia; 5–10 m depth.

Remarks. As mentioned for *P. delwynae*, the taxonomic status between the two Australian species, *P. delwynae* and *P. longistriatus*, is not clear. Both were described from a very restricted area and the morphological variation between them is very subtle. There is a need for a more detailed study approach to understand the differences between these two currently valid species.

Type material. Australian Museum – AM G15402 (Holotype).

35 *Pachycerianthus magnus* (Nakamoto, 1919)

http://zoobank.org/909B29CC-61CA-4766-A000-73FB6FFAFB18

Cerianthus magnus Nakamoto, 1919: 118–120

Pachycerianthus magnus: Uchida 1979: 186–189; Carter 1995: 6; Uchida and Soyama 2001: 125, 151, 152; Molodtsova 2004b: 261; Stampar et al. 2014a: 2; Stampar et al. 2014c: 350, 352; Stampar et al. 2019: 1–9

Type locality. south of Jogashima, Sagami Bay, Miura, Kanagawa, Japan (at 1100 m depth).

Distribution. Japan and China, shallow to deep waters.

Remarks. The description of *Cerianthus magnus* by Nakamoto (1919) is quite adequate, but still very simple. Nevertheless, the author presented a scheme of the mesenteries, and two photos of preserved and dissected material, which allows an adequate comparison with other species. Uchida (1979) moved this species to the genus *Pachycerianthus* and performed a very detailed redescription of the species based on specimens from Sagami Bay, Japan. This species occurs in an area with

several other species of Ceriantharia but is apparently consistent with regard to its taxonomy. The co-occurrence of these species in Sagami Bay may be relevant in an evolutionary context with a focus on environmental niche differentiation among Ceriantharia species.

Type material. Not found in this study, but the original description provided a graphic representation.

36 *Pachycerianthus maua* (Carlgren, 1900)

http://zoobank.org/7797F482-1430-400F-ABD3-7FB2E511A132

Cerianthus maua Carlgren, 1900: 27–29; Krempf 1905: 195; Pax 1909: 413; Pax 1910: 167; Schmidt 1972: 427, 433; Emig et al. 1972: 304–307
Cerianthus mana Fishelson 1970: 109
Pachycerianthus maua: Carlgren 1912b: 389–391; Arai 1971: 1680; Carter 1995: 5; Stampar et al. 2014b: 350, 352

Type locality. Mkokotoni, Zanzibar, Tanzania.

Distribution. Indian Ocean (Mozambique, Madagascar, and Tanzania) and Aden Gulf (Djibouti) and Red Sea (Egypt and Saudi Arabia), shallow waters.

Remarks. This species was described by Carlgren (1900), who subsequently moved this species to the genus *Pachycerianthus* and added some comments on its morphology (Carlgren 1912b). Krempf (1905) recorded two specimens from Djibouti, but he did not study anatomical characteristics. Much later, Fishelson (1970) recorded a great number of specimens from Eilat, Israel. However, again, the author failed to mention any anatomical characters of the specimens, and the figure of the presented specimen is quite inconsistent with the description of Carlgren (1900) or with specimens analyzed from Mozambique (S. Stampar pers. obs.). Thus, the identification of the Red Sea specimens may be misleading, and these Red Sea specimens could be classified either as another species already known to the region (perhaps *Cerianthus medusula*) or as an undescribed species.

Type material. Not found in this study, but the original description provided a graphic representation.

37 *Pachycerianthus monostichus* McMurrich, 1910

http://zoobank.org/CDDC2972-281C-488C-84C4-BD5D468ADFA1

Pachycerianthus monostichus McMurrich, 1910: 38–39; Carlgren 1912a: 44–47; Arai 1971: 1680; van Soest 1979: 118; Carter 1995: 6; den Hartog 1997: 352; Stampar et al. 2014b: 350 352

Type locality. Ambon, Maluku, Indonesia.

Distribution. Only known from shallow water at the type locality.

Remarks. This species was described by McMurrich (1910) based on two specimens from Ambon Island, Indonesia. The information presented by the author is quite suitable for characterization of the species, especially as the mesentery organization is quite conspicuous. No further relevant information on this species is available to date.

Type material. Not found in this study, but the original description provided a graphic representation.

38 *Pachycerianthus multiplicatus* Carlgren, 1912

http://zoobank.org/1D9265CA-F705-4693-B955-D17D0A63500A

Cerianthus membranaceus: Lütken 1889: 362

Cerianthus danielssen: Levinsen 1893: 397; Carlgren 1896: 174

Pachycerianthus multiplicatus Carlgren, 1912a: 5–11; Carlgren 1931: 8–9; Carlgren 1940: 9–12; Carlgren 1942: 70–71; Carlgren 1945: 68–70; Schmidt 1972: 427, 432–433; Arai 1971: 1689; Keegan and Könnecker 1973: 257 Mariscal et al. 1977: 395; Manuel 1981: 64, 67; Picton 1985: 485; McFarlane 1988: 365–370; Carter 1995: 6; Molodtsova 2000: 12, 15, 17; Jonsson et al. 2001: 189–195; Stampar et al. 2014b: 350, 352

(?) *Pachycerianthus multiplicatus*: Çinar et al. 2014: 684

Type locality. Two areas are mentioned – Kattegat Strait and Trondheim, Norway (not specified)

Distribution. North, Inner, Celtic, Irish and Norwegian Seas, Gulf of Biscay, at < 130 m depth.

Remarks. Levinsen (1893) described this species as *Cerianthus danielssen*, however, this description was incomplete and did not meet the minimum characterization requirements for a cerianthid species. Thus, Carlgren (1912a) proposed the new name *P. multiplicatus*, while giving a detailed description of this species. Carlgren (1912b) included several records in the region as well as some biological aspects. Nyholm (1943) gave a detailed study of the life cycle of the species, including information on reproductive seasons and also on larval development (a modified planula). This is a very interesting species for ecological studies, as several reports have mentioned clusters of individuals in different regions (e.g., Jonsson et al. 2001). There is still doubt about the true distribution of the species as individuals recorded from the coast of France and Spain have never been studied in detail.

Type material. (?) Lund Museum of Zoology (MZLU) - 6570 (syntype), but not formally designated in description.

39 *Pachycerianthus nobilis* (Haddon & Shackleton, 1893)

http://zoobank.org/7EE6D6AD-FAF0-447C-A609-D2D03A083096

Cerianthus nobilis Haddon and Shackleton, 1893: 116, 118; Carlgren 1896: 174; Haddon 1898: 400–401; Pax 1910: 167

Pachycerianthus nobilis: Molodtsova 2000: 19; Molodtsova 2007: 133; Stampar et al. 2014b: 350, 352

Type locality. Thursday Island, Queensland, Australia.

Distribution. Queensland and Northern Territory, Australia, New Caledonia, shallow waters.

Remarks. A large species originally described from northeastern Australia as *Cerianthus nobilis*. This description is very simple and was based only on external characters and there have been no further studies based on specimens from this area. Molodtsova (2000, 2007) correctly suggest that this species does not belong to the genus *Cerianthus*, but to the genus *Pachycerianthus*. The relation with two species described by Carter (1995) (*P. delwynae* and *P. longistriatus*) is completely unknown, however, there is the possibility that all three species are, in fact, a single one, based on their overlapping morphological characters.

Type material. Museum of Zoology (University of Cambridge) – I.33575.A-B (holotype).

40 *Pachycerianthus schlenzae* Stampar, Morandini & Silveira, 2014
http://zoobank.org/7D2022C6-CE8E-4FC4-B54D-39ED0006FA7F

Pachycerianthus sp. Vieira and Stampar 2014: 365, 367–368, 370–371
Pachycerianthus schlenzae Stampar et al., 2014b: 343–354

Type locality. off Guarapari, Espírito Santo state, Brazil.

Distribution. Brazil, from Bahia to Espírito Santo states (Abrolhos Bank and Royal Charlotte Bank), at 5–10 m depth.

Remarks. This species was recently described based on a study of several specimens from the central area of the Brazilian coast, where it is an endemic occurring along a coastline of approximately 500 km length. Some aspects of external morphology are similar to those of *P. curacaoensis* and may reflect a correlated evolutionary history between the two species. Although Stampar et al. (2014b) presented some biological information mainly related to the reproduction seasons, little is known about the ecology and biology of this species. The species is endangered as its range suffers from high levels of anthropogenic pressure (Miranda and Marques, 2016), which could result in the loss of its habitat.

Type material. Museu de Zoologia, Universidade de São Paulo (MZSP) – 1949 (Holotype).

41 *Pachycerianthus solitarius* (Rapp, 1829)
http://zoobank.org/DDC053BF-7A9C-4CB8-9126-FE701530AB39

Tubularia solitaria Rapp, 1829a: 656–658; Rapp 1829b: 48–49

(?) *Cereus cupreus* Ilmoni, 1830: 689–699; Ilmoni 1831: 123
Cerianthus brerae Delle Chiaje, 1841: 136
Edwardsia vestita Forbes, 1843: 42; Milne-Edwards 1857: 286
Cerianthus membranaceus: Sars 1857: 28–32; Heller 1868: 20, 79
Cerianthus solitarius: Andres 1881: 332; Andres 1883: 345–346; Fischer 1887: 384–385, 432, 437; Fischer 1889: 254, 264, 265; Faurot 1895: 221; van Beneden 1897: 138; Child 1903a: 239–260; Child 1903b: 8–10; Child 1904a: 70–71; Child 1904b: 266–284; Gravier 1904: 283; Rioja and Martin 1906: 280; Cerfontaine 1909: 699–700; McMurrich 1910: 17–18; Pax 1910: 166; Mello-Leitão 1919: 35–36, 39; van Beneden 1924: 29, 89–96; Torelli 1961: 17–28
Pachycerianthus solitarius: Carlgren 1912a: 367–387; Carlgren 1912b: 44–47; Carlgren 1927: 443; Panikkar 1936: 259; Pax and Müller 1962: 110; Torelli 1963: 175–177; Naumov 1968: 73; Arai 1971: 1680; Uchida 1979: 188; Williams 1981: 350; Ates 1985: 230–231; Carter 1995: 6; Molotsova 2003: 250, 252–253; Çinar et al. 2014: 684
(?) *Pachycerianthus solitarius*: Kisseleva 1975: 1595–1596; Wirtz et al. 2003: 115, 116
Cerianthus bicyclus Torelli, 1961: 17–28

Type locality. off Languedoc coast, France.

Distribution. Mediterranean Sea, Azores, and (?) Black Sea; shallow waters.

Remarks. After *Cerianthus membranaceus*, this was the second species to be formally described in Ceriantharia. It was first described as an unclassified polyp with some similarities with Hydrozoa and Anthozoa (Rapp 1829a). Later, it was only characterized as a Ceriantharia by Sars (1857). This species was widely studied by Child (1903a, 1903b, 1904a, 1904b) in a series of experimental studies related to asexual reproduction, behavior, and regeneration of polyps. Carlgren (1912b) presented a detailed redescription of this species and moved it to the genus *Pachycerianthus*. He described several abnormalities of the species' anatomy (Carlgren 1912a), which were attributed to asexual reproduction events that are uncommon in Ceriantharia. After this, several authors reported this species from various regions, including the Black Sea (Kiseleva 1975). If *P. solitarius* occurs in the Black Sea, it would show a great tolerance to brackish water. Therefore, specimens recorded in the Black Sea may not be of the same species that inhabits the Mediterranean Sea. However, there are no available specimens for comparison. Wirtz et al. (2003) recorded this species in the Azores, however a more detailed study is needed to understand if this species occurs outside the Mediterranean Sea, or whether the Azores specimens belong to *P. solitarius*.

Type material. Not found in this study.

Family Botrucnidiferidae Carlgren, 1912

Number of valid taxa: two genera and four species.

Genus *Botruanthus* McMurrich, 1910

Table 5

Type species. *Botruanthus benedeni* (Torrey & Kleeberger, 1909)

Number of valid species: 2

42 *Botruanthus benedeni* (Torrey & Kleeberger, 1909)

http://zoobank.org/B663D1F1-44EB-4EBC-8644-729518D0104A

*Pachyceri*anthus benedeni Roule, 1904: 708–710

Cerianthus benedeni: Torrey and *Kleeberger 1909: 115*, 119, 120–123, 125; Pax 1910: 167;

Bo*tryanthus benedeni: McMurrich 1910: 11; Torelli 1932: 9*

Botruanthus benedeni: Carlgren 1912a: 44–47; Leloup 1932: 17; Carlgren 1951: 431, 433–435; Arai 1965: 205; den Hartog 1977: 211, 233, 236–237; Molodtsova 2001c: 1027, 1033–1035; Fautin et al. 2007: 551–552, 567–569; Stampar et al. 2016b: 1; 5

Type locality. San Diego Bay, California, United States of America.

Distribution. California (United States of America), Baja California (Mexico) and Galapagos Islands (Ecuador), shallow waters.

Remarks. This species was described based on a study of a single specimen. This species (and genus) is characterized by possessing wart-like structures (cnidorages) organized in bunches (botrucnids) in the mesenterial filaments. Except for these structures, the anatomy is very similar to species of the genus *Pachycerianthus*. The holotype is not available, and we therefore here designate a neotype collected from the same region by Charles Cutress in 1955 (NMNH 49400). This specimen was studied by Stampar et al. (2017) (erroneously referred to as "holotype") and its characters are consistent with those in the original description. Because of its importance as type species of the genus *Botruanthus*, the neotype designation for this species is justified. This is a poorly studied genus and there is no biological or ecological information about this species.

Type material. Smithsonian National Museum of Natural History (USNM) – 49400 (neotype).

43 *Botruanthus mexicanus* Stampar, González-Muñoz & Morandini, 2017

http://zoobank.org/61DE065D-E0EB-4BE4-A283-E7EADFCD7262

Botruanthus mexicanus Stampar et al., 2017: 113–118

Type locality. off Veracruz, Mexico.

Table 5. Comparison of anatomical features of *Botruanthus* species (after Stampar et al. 2016a).

	B. benedeni	***B. mexicanus***
Marginal tentacles	Up to 90–100	Up to 40–60
Directive labial tentacle	Present	Present
Arrangement of labial tentacles	(1)321.3213.3213	(2)314.2314.2314.2314
Actinopharynx	1/3 – 1/4 of gastric cavity	1/5–1/4 of gastric cavity
Oral disc	1.1–1.3 cm	0.5–0.7 cm
Siphonoglyph	Broad, 8 mesenteries attached	Narrow, 2 mesenteries attached
Directive mesenteries	>Actinopharynx (= size of Actinopharynx)	> Actinopharynx
P2	Long, almost to aboral pole (> 2/3 of gastric cavity)	Short (<1/3 of gastric cavity)
P3	Short (1/3 of P2)	Short (~P2)
M1	To aboral pore	Almost to aboral pore
M3	Almost to aboral pore	Short, 1/2 of M1
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present
Craspedion tract at fertile mesenteries	5/7–8/9	8/9
Cnido-glandular tract at B	< ½	3/4
Craspedonemes of craspedion at fertile mesenteries	Sometimes present	Sometimes present
Botrucnidae	Rare in m and B, absent in M and b mesenteries	Very abundant (4-5 groups) in M and m, absent in B and b mesenteries

Distribution. Gulf of Mexico, intertidal to shallow waters.

Remarks. This species was recently described by specimens from the intertidal zone in reefs of Central Mexico in the Gulf of Mexico. Morphological characterization is quite easy, as the number of anatomical characters allow its distinction in relation to *B. benedeni*. There have been no studies on ecological or biological aspects of this species.

Type material. Museu de Zoologia da Universidade de São Paulo; MZUSP 002757 (Holotype).

Genus *Botrucnidifer* Carlgren, 1912

Table 6

Type species. *Botrucnidifer norvegicus* Carlgren, 1912

Number of valid species: two

44 *Botrucnidifer norvegicus* Carlgren, 1912

http://zoobank.org/5D96E928-EB37-4362-ADD0-F20293438F44

Botrucnidifer novergicus Carlgren, 1912a: 30–34; Carlgren 1931: 10; Leloup 1932: 16–18; Carlgren 1940: 6,10,14–15; Carlgren 1942: 70–71; Carlgren 1945: 72;

Table 6. Comparison of anatomical features of *Botrucnidifer* species.

	B. novergicus	*B. shtokmani*
Marginal tentacles	Up to 17	72
Directive labial tentacle	Present	Absent
Arrangement of labial tentacles	(1)431.3231.3231	(0)230.2024.3123.3142
Actinopharynx	1/4 – 1/5 of gastric cavity	1/3 of gastric cavity
Oral disc	0.3 cm	1.5 cm
Siphonoglyph	Narrow, 2 mesenteries attached	Narrow, 4 mesenteries attached
Directive mesenteries	>Actinopharynx	= Actinopharynx
P2	Long, almost to aboral pole (> 4/5 of gastric cavity)	Regular (<2/3 of gastric cavity)
P3	Long (2/3 of P2)	Short, 1/2 of P2
M1	Almost to aboral pore	= P2
M3	Almost to aboral pore (3/4 of M1)	Long, 3/4 of P2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present
Craspedion tract at fertile mesenteries	¾	1/2 – 3/4
Cnido-glandular tract at B	Present	Present
Botrucnidae	Only in M mesenteries	Only in B/b mesenteries

Nair 1949: 245; den Hartog 1977:136; Molodtsova 2000: 14–17; Molodtsova 2001c: 1027, 1033–1036; Molodtsova 2004a: 292–293, 295–296; Stampar et al. 2016c: 2,4; Ceriello et al. 2019: 2017–2020

Type locality. Trondheimfjord, Trondheim, Norway.

Distribution. Norwegian Sea, at 50–700 m depth.

Remarks. This species was described by Carlgren (1912a) based on specimens from Trondheim Fjord, Norway. These are small ceriantharians (up to 4 cm long) with an expansion of the cnidoglandular tract and some botrucnidae (= cnidoragae) at the end of some mesenteries. Although the description is fairly comprehensive, knowledge of this species is limited. Other authors cite only some of the species characteristics or have reported occurrences in areas that look similar (e.g., Molodtsova 2004a). Recently, Ceriello et al. (2019) reported on the coloniality of this species, which is a newly discovered trait among Ceriantharia. This species is important in the discussion on the homology of morphological characters, particularly in relation to mesenterial structures.

Type material. Lund Museum of Zoology (MZLU) – L898/3051 and Marine invertebrate collection Norwegian University of Science and Technology University Museum (NTNU) – 40499 (syntype).

45 *Botrucnidifer shtokmani* Molodtsova, 2001

http://zoobank.org/2B2E3575-21EB-4B85-80AA-817B45BB89A1

Botrucnidifer shtokmani Molodtsova, 2001a: 773; Molodtsova 2001c: 1027–1036; Molodtsova et al. 2011: 1

Type locality. off Namibia coast (southeast Atlantic), at 130–350 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species was described based on dredged specimens from off the Namibian coast. This is the second species of this genus that has been sampled beyond conventional SCUBA diving depths. The description of this species (in Russian) is very detailed and addresses all the necessary characters. As discussed by Molodtsova (2001c) some larval forms of this family are recognized from this area, however the link between larval and adult stages is only possible based on molecular or developmental approaches (Nyholm 1943; Stampar et al. 2015c).

Type material. Zoological Museum of Moscow University – ZMMU EC-100 (holotype).

Order Penicillaria den Hartog, 1977

Number of valid taxa: one family, two genera, and nine species

Family Arachnactidae McMurrich, 1910

Number of valid taxa: two genera, and nine species

Genus *Arachnanthus* Carlgren, 1912

Table 7

Type species. *Arachnanthus oligopodus* (Cerfontaine, 1891)

Number of valid species: Five

46 *Arachnanthus australiae* Carlgren, 1937

http://zoobank.org/249FDE31-6249-45B8-8930-D87A827BC87B

Arachnanthus australiae Carlgren, 1937: 177–180; den Hartog 1977: 235; Fautin et al. 2007: 570; Stampar et al. 2018: 3,8

Type locality. Low Isles, Queensland, Australia.

Distribution. Queensland, Australia, shallow waters.

Remarks. Carlgren (1937) described this species from northeastern Australia and this is the only study so far on this species. Although the description is adequate, it does not include detailed information. In general, the Australian coast is vastly understudied regarding Ceriantharia species diversity. The taxonomic status of *A. australiae* in relation to *Arachnanthus bockii* remains to be studied in detail.

Table 7. Comparison of anatomical features of *Arachnanthus* species (after Stampar et al. 2018).

	A. australiae	*A. bockii*	*A. oligopodus*	*A. sarsii*	*A. lilith*
Marginal tentacles	Up to 40	Up to 30	~20	Up to 35	Up to 24
Arrangement of labial tentacles	(0)1.11.11.11.11	(0)1.11.11.11.11(?)	(0)1.11.11.11.11	(0)1.11.11.11.11	(0)3.12.31.23.23.12
Length of actinopharynx	~2/3 of gastric cavity	~1/2 of gastric cavity	~1/2 of gastric cavity	~1/2 of gastric cavity	>1/2 of gastric cavity
Hyposulcus	~1/2 size of stomodeum	~1/2 size of stomodeum	~2X size of stomodeum	< size of stomodeum	= size of stomodeum
Oral disc diameter	~0.7 cm	–	–	~1 cm	0.5 cm
Mesentery attachment to actinopharynx	Broad, 12 mesenteries attached	Broad, 12 mesenteries attached	Narrow, 4 mesenteries attached	Broad, 6 mesenteries attached	Broad, 8 mesenteries attached
Directive mesenteries	= length of Actinopharynx	< length of Actinopharynx	> length of Actinopharynx	< length of Actinopharynx	< length of Actinopharynx
P(C)2	Short, 1/2 of gastric cavity	Very short, 1/4 of gastric cavity	Short, 1/2 of gastric cavity	Long, 3/4 of gastric cavity	Long, 6/7 of gastric cavity, almost to aboral pole
P(C)3	Very short, <1/4 of gastric cavity	Very short, <1/4 of gastric cavity	Short, ~1/2 of gastric cavity	Short, ~1/3 of gastric cavity	Short, 1/3 of gastric cavity
M1	Almost to aboral pore	Almost to aboral pore	To aboral pore	Almost to aboral pore	To aboral pore
M3	4/5 of gastric cavity	Almost to aboral pore	1/5 of gastric cavity	Almost to aboral pore	3/4 of gastric cavity
Cnido-glandular tract of fertile mesenteries	Present (short?)	Present (short?)	Present	Present	Present
Cnido-glandular tract of B	Present (short?)	Present (short?)	Present (short?)	Present (short)	Present (short)
Acontioids	Only in M1, M2 and M3	Only in M1, M2 and M3	Only in M1	Only in M1, M2 and M3	Only in M3 and M4

Type material. Natural History Museum (London); NHMUK – 1954.6.25.47 (holotype).

47 *Arachnanthus bockii* Carlgren, 1924

http://zoobank.org/357544F3-9111-420C-B6AD-B9A446BB9451

Arachnanthus bockii Carlgren, 1924: 193–195; den Hartog 1977: 235

Type locality. Viti Levu, Fiji.

Distribution. Only known from shallow water at the type locality.

Remarks. This is another species with little information, except for the morphological description. There are some characters in Carlgren's (1924) description that allows distinction of this species in comparison to *Arachnanthus australiae*, however,

the reduced number of specimens may be a problem to understand the intraspecific variation of these characters.

Type material. Not found in this study, but the original description provided a graphic representation.

48 *Arachnanthus oligopodus* (Cerfontaine, 1891)

http://zoobank.org/7B2B79CA-DC0A-4E14-9ED0-06F2AB20C245

Cerianthus oligopodus Cerfontaine, 1891a: 32–38; Carlgren 1895: 284; van Beneden 1897:140; Gravier 1904: 286; Cerfontaine 1909: 653–707; McMurrich 1910a: 165; Pax 1910: 166; Mello-Leitão 1919: 36, 39; van Beneden 1924: 12, 20, 30, 45, 92, 97, 98; Torelli 1932:12; Torelli 1961: 17–28

Pachycerianthus oligopodus: McMurrich 1910b: 11–13

Arachnanthus oligopodus: Carlgren 1912a: 367–388; Carlgren 1912b: 44–47; Panikkar 1947: 243; Leloup 1960: 2; den Hartog 1977: 235; Vafidis and Koukouras 1998: 123–124; Molodtsova 2003: 253; Çinar et al. 2014: 677, 683, 687, 688; Rastorgueff et al. 2015: 142, 148

Type locality. Italian Coast, Mediterranean Sea (not specified in detail).

Distribution. Mediterranean Sea, shallow waters and caves.

Remarks. *Arachnanthus oligopodus* was initially described as a species of the genus *Cerianthus* by Cerfontaine (1891a), and was moved to the genus *Arachnanthus* by Carlgren (1912b). This is a very common species in several areas of the Mediterranean Sea, especially on the Italian Coast (Carlgren 1924; Torelli 1961). This species has a number of descriptions with appropriate levels of detail (e.g., Cerfontaine 1909; Carlgren 1912a). However, knowledge of the species is still incipient. Biological aspects, especially on the life cycle, are still quite unknown.

Type material. Not found in this study.

49 *Arachnanthus lilith* Stampar & El Didi in Stampar et al. 2018

http://zoobank.org/fc381c67-9db8-4280-9c9c-00dbd04f7d56

Arachnanthus lilith Stampar and El Didi in Stampar et al. 2018: 1–7

Type locality. island near Jaz'air Sila, Saudi Arabia.

Distribution. Red Sea, shallow waters.

Remarks. This species was recently described from shallow Saudi Arabian waters of the Red Sea. Morphological characterization was based on internal anatomy and there have been no studies on ecological or biological aspects of this species yet.

Type material. Florida Museum of Natural History – FLMNH UF9168 (holotype).

50 *Arachnanthus sarsi* Carlgren, 1912

http://zoobank.org/04EE6C07-87AA-4137-8391-D6FE93024EFB

Arachnanthus sarsi Carlgren, 1912a: 27–30; Carlgren 1942: 70–71; Nair 1949: 243; Picton and Manuel 1985: 343–349; Picton 1985: 485–486; Molodtsova 2000: 15, 17; Molodtsova 2003: 251; Stampar et al. 2015c: 2164
Arachnanthus sarsii: Carlgren 1931: 9–10; Carlgren 1940: 6, 11, 13, 15

Type locality. Röberg Indalbay, Trondheim, Norway.

Distribution. North Sea, at 10–200 m depth.

Remarks. This species is rather common in some areas of Great Britain and Scotland and there are two detailed descriptions; the original (Carlgren 1912b) and a redescription (Picton and Manuel 1985). The life cycle has been inferred from the occurrence of larvae named as *Arachnactis albida* (Picton and Manuel 1985), but further study is needed to understand the relationship in detail. Not much is known about ecological aspects of this species and this should be a very interesting field of study.

Type material. Swedish Museum of Natural History (Naturhistoriska riksmuseet) – NRM 134778 (Holotype).

Genus *Isarachnanthus* Carlgren, 1924

Table 8

Type species. *Isarachnanthus maderensis* (Johnson, 1861)

Number of valid species: 4

51 *Isarachnanthus bandanensis* Carlgren, 1924

http://zoobank.org/66c30a7f-149e-4c92-8a8d-c7a63fe71194

Isarachnanthus bandanensis Carlgren, 1924: 187–190, 195; Cutress 1977: 145; den Hartog 1977: 235; Cutress and Arneson 1987: 54, 56–58; den Hartog 1997: 352; Stampar et al. 2012: 1–2, 5–9.

Type locality. Neira, Banda Island, Indonesia.

Distribution. Indonesia, French Polynesia, and Hawaii (USA), shallow waters.

Remarks. This species was described based on two specimens from the Banda Islands, Indonesia. The diagram of mesenteries, part of cnidome, and tentacle organization are present in the original description, however, there are some evident similarities in relation to *Isarachnanthus panamensis*. Furthermore, unpublished molecular data indicate similarity between these two species and studies on this clade should be prioritized.

Type material. Zoological Museum of Amsterdam (now Naturalis Biodiversity Center, Leiden) – (ZMA.COEL.000209 – Lectotype/ ZMA.COEL.000210 – Paralectotype).

52 *Isarachnanthus maderensis* (Johnson, 1861)

http://zoobank.org/B6923781-7CEE-4F15-89C6-A35765626176

Saccanthus maderensis Johnson, 1861: 305–306; Andres 1883: 346
Cerianthus maderensis: Pax 1908: 262–263;
In part *Cerianthus membranaceus* Pax 1908: 464–465, 497–498
Arachnanthus nocturnus: Ocaña et al. 2000b: 107; Wirtz et al. 2003: 114–116
Isarachnanthus cruzi Brito, 1986: 174–181
? *Cerianthus* sp. Torelli 1963: 714–715
Isarachnanthus maderensis: Molodtsova 2003: 249–253; Stampar et al. 2012: 1–9; Stampar and Morandini 2017: 689–693

Type locality. Madeira Island, Portugal.

Distribution. Madeira Island (Portugal), Ascension Island, Rocas Atoll (Brazil), Caribbean Sea, (?) Mediterranean Sea; at 2–30 m depth.

Remarks. This species was described by Johnson (1861) from Madeira Island. However, the first detailed morphological characterization was presented by Brito (1986) (as *I. cruzi*). The delimitation of this species is quite complicated, as according to Stampar et al. (2012) only molecular data or morphometric data of the cnidome can be used to compare to other species of the genus. The distribution of this species is quite wide, from oceanic islands of the South Atlantic to the Caribbean Sea and the Mediterranean Sea (Stampar and Morandini 2017).

Type material. Not found in this study.

53 *Isarachnanthus nocturnus* (den Hartog, 1977)

http://zoobank.org/07411A5F-9150-4FDD-9080-565F5C4A8D00

Cerianthus natans: Verrill 1901: 47
Ceriantheopsis sp. Pax 1924: 94, 118–120
Arachnanthus nocturnus den Hartog, 1977: 221–230; Cairns et al. 1986: 192–193; Uchida and Soyama 2001: 142, 150, 152 Wirtz et al. 2003: 115–116;
Isarachnanthus nocturnus: Molodtsova 2000: 15,17; Molodtsova 2003: 251–252; Stampar et al. 2012: 1–9
Isarachnanthus sp. Rodriguez et al. 2011: 51; 52, 54
Tessera gemmaria Goy, 1979: 288–289; Rodriguez et al. 2011: 51–55; Stampar et al. 2015c: 2162

Type locality. Piscadera Bay, Curaçao, Dutch Caribbean.

Table 8. Comparison of anatomical features of *Isarachnanthus* species.

	I. bandanensis	*I. maderensis*	*I. nocturnus*	*I. panamensis*
Marginal tentacles	Up to 40	Up to 42	Up to 60	Up to 32
Arrangement of labial tentacles	(3)413.4242.4312.4312	(1)1.11.11.11.11	(1)2.12.12.12.12	(2)431.4231.4231
Length of actinopharynx	~1/4 of gastric cavity	~2/5 of gastric cavity	~2/5 of gastric cavity	~1/2 to 1/3 of gastric cavity
Hyposulcus	~2/3 size of stomodeum	= size of stomodeum	= size of stomodeum	= size of stomodeum
Oral disc diameter	~2cm	2 cm	3.5 cm	~0.5 cm
Mesentery attached to siphonoglyph	Broad, 18 mesenteries attached	Broad, 10 mesenteries attached	Broad, 12-14 mesenteries attached	Broad, 16 mesenteries attached
Directive mesenteries	= length of Actinopharynx	> length of Actinopharynx	> length of Actinopharynx	>length of Actinopharynx
P(C)2	Long, 3/4 of gastric cavity	Short, 1/3 of gastric cavity	Short, 1/3 of gastric cavity	Long, 3/4 of gastric cavity
P(C)3	Very short, <1/8 of gastric cavity	Very short, ~1/6 of gastric cavity	Very short, ~1/5 of gastric cavity	Short, ~1/5 of gastric cavity
M1	Almost to aboral pore	Almost to aboral pore	Almost to aboral pore	Reach aboral pore
M3	Almost to aboral pore	Almost to aboral pore	Almost to aboral pore	Reach aboral pore
Cnido-glandular tract of fertile mesenteries	Present (short?)	Present	Present	Present (short?)
Cnido-glandular tract of B	Present (short?)	Present (short)	Present (short)	Present (short?)
Acontioids	Only in M1- M4	Only in M1-M6	M1-M3 (sometimes in M4 and M5)	Only in M1- M5 or absent

Distribution. Caribbean Sea, South Atlantic (Argentina; Brazil), at 1–20 m depth.

Remarks. This species was described by den Hartog (1977) based on specimens from Curaçao. The specific epithet is related to the nocturnal behavior of this species. This is the most studied species of the genus, as the larval development has been described and the taxonomy has been reviewed with molecular data (Stampar et al. 2012, 2015c). Molodtsova (2003) argued that this species is only a synonym of *Isarachnanthus maderensis*, however, based on molecular and micrometric data (Stampar et al. 2012) it has been shown that these two species are distinct.

Type material. Naturalis Biodiversity Center, Leiden (former Rijksmuseum van Natuurlijke Historie) – RMNH.COEL.11364 (Holotype).

54 *Isarachnanthus panamensis* Carlgren, 1924

http://zoobank.org/CB322F62-0E21-4157-9107-4279DA1E16A9

Isarachnanthus panamensis Carlgren, 1924: 190–193, 195; Carlgren 1940: 6, 11, 13–14; Molodtsova 2003: 251; Stampar et al. 2012: 1–2

Type locality. Taboga, Panama (Pacific coast).

Distribution. Only known from shallow water at the type locality

Remarks. This species was described from the Panama coast based on three specimens. The description is also detailed, including two mesentery diagrams. Thus, variation in mesenterial organization is quite evident, especially in relation to the size of directive mesenteries. As discussed above, regarding *Isarachnanthus bandanensis*, these two species are very similar in terms of both morphological and molecular data and further studies are needed.

Type material. Zoological Museum of Amsterdam (now Naturalis Biodiversity Center, Leiden) – ZMA.COEL .000211) (holotype).

Key to species

* Species with limited information on their anatomy, therefore key must be used with caution.

1a Ceriantharia with mesenteries organized in doublets (Spirularia) **2**

1b Ceriantharia with mesenteries organized in quartets (Penicillaria) **16**

2a Ceriantharia with cnidorage (botrucnidae)..... **3**

2b Ceriantharia without cnidorage (botrucnidae) **6**

3a Cnidorage on appendages united as botrucnidae..... **4**

3b Cnidorage over mesenteries..... **5**

4a P-mesenteries (P2) and M-mesenteries (M3) long, almost to aboral pore..... ..... ***Botruanthus benedeni*** **(Torrey & Kleeburger, 1909)**

4b P-mesenteries (P2) and M-mesenteries (M3) short, 1/2 to 1/3 of gastric cavity... ..... ***Botruanthus mexicanus*** **Stampar, González-Muñoz & Morandini, 2016**

5a Directive mesenteries much longer than hyposulcus .... ***Botrucnidifer novergicus*** **Carlgren, 1912**

5b Directive mesenteries shorter or equal than hyposulcus..... ..... ***Botrucnidifer shtokmani*** **Molodtsova, 2001**

6a Ceriantharia with all mesenteries except directives fertile **7**

6b Ceriantharia with second couple of protomesenteries (P) short and sterile.... **8**

6c Ceriantharia with second couple of protomesenteries (P) long and fertile, mesenteries in quartets m, B, M, b..... **11**

6d Ceriantharia with second couple of protomesenteries (P) long and fertile, mesenteries in quartets M, B, m, b..... **12**

7a Directive mesenteries of the same length as protomesenteries 3 (P3)..... ..... ***Ceriantheomorphe brasiliensis*** **(Mello-Leitão, 1919)**

7b Directive mesenteries shorter than protomesenteries 3 (P3) .... ***Ceriantheomorphe ambonensis*** **(Kwietniewski, 1898)**

7c Directive mesenteries longer than protomesenteries 3 (P3)... ***Ceriantheomorphe adelita*** **Lopes, Morandini & Stampar in Lopes et al., 2019**

8a Number of marginal tentacles – less than 90..... **9**

8b Number of marginal tentacles – more than 115..... **10**

9a Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and 6 mesenteries attached to siphonoglyph ..... ***Pachycerianthus schlenzae*** **Stampar, Silveira & Morandini, 2014**

9b Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and more than 90 marginal tentacles ..... ***Pachycerianthus johnsoni*** **(Torrey & Kleeburger, 1909)**

9c Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and less than 70 marginal tentacles ..... ***Pachycerianthus fimbriatus*** **(Kwietniewski, 1898)**

9d Metamesenteries 2 (M2) longer than half of metamesenteries 1 (M1) and 4 mesenteries attached to siphonoglyph ..... ***Pachycerianthus curacaoensis*** **den Hartog, 1977**

9e Metamesenteries 2 (M2) longer than metamesenteries 1 (M1), 6 mesenteries attached to siphonoglyph and directive labial tentacle present..... ***Pachycerianthus delwynae*** **Carter, 1995**

9f Metamesenteries 2 (M2) longer than Metamesenteries 1 (M1) and 16 mesenteries attached to siphonoglyph ..... ***Pachycerianthus aestuarii*** **(Torrey & Kleeburger, 1909)**

9g Metamesenteries 2 (M2) and metamesenteries 1 (m1) longer than metamesenteries 1 (M1) and 8 mesenteries attached to siphonoglyph ..... ***Pachycerianthus insignis*** **Carlgren, 1951**

9h Metamesenteries 2 (M2) and metamesenteries 2 (m2) longer than metamesenteries 1 (M1) and 8 mesenteries attached to siphonoglyph ..... ***Pachycerianthus monostichus*** **McMurrich, 1910**

9i Metamesenteries 1 (m1) longer than ¼ of Metamesenteries 1 (M1) and 6 mesenteries attached to siphonoglyph ..... ***Pachycerianthus solitarius*** **van Beneden, 1924**

10a Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than than ¾ of M1 ..... ***Pachycerianthus borealis*** **Kingsley, 1904**

10b Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1, labial directive tentacle present ..... ***Pachycerianthus longistriatus*** **Carter, 1995**

10c Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1 ..... ***Pachycerianthus magnus*** **Uchida, 1979**

10d Metamesenteries 2 (M2) longer than 1/4 of metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1 ..... ***Pachycerianthus maua*** **Carlgren, 1900**

10e Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1, labial directive tentacle absent..... ***Pachycerianthus multiplicatus*** **Carlgren, 1912**

10f Polyp with more than 160 tentacles from Australia ..... ***Pachycerianthus nobilis*** **(Haddon & Shackleton, 1894)**

10g Polyp with more than 160 tentacles from Mediterranean Sea ..... ***Pachycerianthus dohrni*** **van Beneden, 1924**

11a Polyp with up to 60 marginal tentacles and directive labial tentacle absent ..... . ***Ceriantheopsis lineata*** **Stampar, Scarabino, Pastorino & Morandini, 2015**

11b Polyp with up to 70 marginal tentacles and cnido-glandular tract at fertile mesenteries present ..... ***Ceriantheopsis austroafricana*** **Molodtsova, Griffiths & Acuña, 2011**

11c Polyp with up to 70 marginal tentacles and cnido-glandular tract at fertile mesenteries absent ..... ***Ceriantheopsis nikitai*** **Molodtsova, 2001**

11d Polyp with more than 90 marginal tentacles and short directive mesenteries. ..... ***Ceriantheopsis americana*** **(Agassiz in Verrill, 1864)**

12a Polyp from India (shallow waters) with more than 150 marginal tentacles .... ***Cerianthus andamanensis*** **Alcock, 1893***

12b Polyp from India (deep sea ~ 5000 m) with up to 40 marginal tentacles and directive labial tentacle absent ..... ***Cerianthus valdiviae*** **Carlgren, 1912***

12c Polyp from North Atlantic (deep sea ~ 5000 m) with up to 30 marginal tentacles ..... ***Cerianthus bathymetricus*** **Moseley, 1877***

12d Polyp from Red Sea (shallow waters) with up to 20 marginal tentacles..... ***Cerianthus medusula*** **(Klunzinger, 1877)***

12e Description with information about mesentery organization and tentacle distribution **13**

13a Species from Pacific Ocean **14**

13b Species from Atlantic Ocean **15**

14a Protomesenteries 2 (P2) short, sterile and metamesenteries 1 (M1) reach or almost reach the aboral pore, marginal/ labial tentacles in 4 pseudocycles ..... ***Cerianthus (?) mortenseni*** **Carlgren, 1924**

14b Polyp from Japan, Korea or China, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 3 ..... ***Cerianthus filiformis*** **Carlgren, 1924**

14c Polyp from Japan, marginal tentacles in 3 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2..... ***Cerianthus japonicus*** **Carlgren, 1924**

14d Polyp from Japan, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2..... ***Cerianthus punctatus*** **Uchida, 1979**

14e Polyp from Indonesia, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2 ..... ***Cerianthus sulcatus*** **Kwietniewski, 1898**

14f Polyp from Indonesia, marginal tentacles in 2 pseudocycles and directive in position 1, labial tentacles in 4 pseudocycles and directive in position 2 ..... ***Cerianthus taedus*** **McMurrich, 1910**

15a Polyp from North Sea/North Atlantic, directive labial tentacle absent, 4 mesenteries attached to siphonoglyph ..... ***Cerianthus lloydii* Gosse, 1859**

15b Polyp from Mediterranean Sea and Central Atlantic, directive labial tentacle present, 6 mesenteries attached to siphonoglyph ..... ***Cerianthus membranaceus* (Gmelin, 1791)**

15c Polyp from Norwegian Sea, directive labial tentacle present, 4 mesenteries attached to siphonoglyph..... ***Cerianthus vogti* Danielssen, 1890**

15d Polyp from Namibia, mesenteries type M and m and P2 are almost of the same size ..... ***Cerianthus malakhovi* Molodtsova, 2001**

16a Directive labial tentacle present..... **17**

16b Directive labial tentacle absent..... **18**

17a Polyp from Atlantic Ocean, microbasic P-mastigophore absent in column.... ..... ***Isarachnanthus nocturnus* (den Hartog, 1977)**

17b Polyp from Atlantic Ocean, microbasic P-mastigophore present in column... ..... ***Isarachnanthus maderensis* (Johnson, 1861)**

17c Polyp from Pacific Ocean, directive labial tentacle in position 2..... ..... ***Isarachnanthus panamensis* Carlgren, 1924**

17d Polyp from Pacific Ocean, directive labial tentacle in position 3..... ..... ***Isarachnanthus bandanensis* Carlgren, 1924**

18a Polyp with 6 mesenteries attached to actinopharynx, protomesenteries 2 (P2) long (3/4 of gastric cavity) ..... ***Arachnanthus sarsi* Carlgren, 1912**

18b Polyp with 4 mesenteries attached to actinopharynx, protomesenteries 2 (P2) short (1/2 of gastric cavity) .... ***Arachnanthus oligopodus* (Cerfontaine, 1891)**

18c Polyp with 12 mesenteries attached to actinopharynx, protomesenteries 2 (P2) very short (1/4 of gastric cavity) ..... ***Arachnanthus bockii* Carlgren, 1924**

18d Polyp with 12 mesenteries attached to actinopharynx, protomesenteries 2 (P2) short (1/2 of gastric cavity)..... ***Arachnanthus australiae* Carlgren, 1937**

18e Polyp with 8 mesenteries attached to actinopharynx, protomesenteries 2 (P2) long (almost to aboral pole) .... ***Arachnanthus lilith* Stampar & El Didi in Stampar et al. 2018**

The species *Cerianthus incertus*, *Cerianthus roulei*, *Cerianthus vas* and *Cerianthus stimpsonii* are not included in key due to absence of characters.

Acknowledgements

This work was supported by São Paulo Research Foundation FAPESP 2015/24408-4, 2016/50389-0, 2019/03552-0, CNPq (PROTAX) 440539/2015-3 and CNPq (Research Productivity Scholarship) 301293/2019-8 to SNS, FAPESP 2016/04560-9 to MMM, FAPESP 2015/21007-9 and CNPq 309440/2019-0 to ACM, and FAPESP 2018/07622-0, 2019/14236-2 to TBS. SNS, HC and CL were supported by CAPES/CNPQ; PROTAX II 88887.301759/2018-00. SNS was also supported

by Australian Museum and Research Institute (AMRI) Visiting Collection Fellowship. We are grateful to several curators and researchers who helped with information or providing access to materials (Dr Stephen Keable (Australian Museum), Dr Sadie Mills (NIWA Invertebrate Collection), Dr Bert Hoeksema (Naturalis Biodiversity Center), Dr Torkild Bakken (NTNU University Museum), Dr Kensuke Yanagi (Natural History Museum and Institute Chiba), Dr So Ishida (Osaka Museum of Natural History), Dr Takuma Fujii (Kagoshima University), Dr Danwei Huang, Dr Neo Mei Lin and Dr Nicholas Yap (National University of Singapore), Dr Priscila Grohmann (Universidade Federal do Rio de Janeiro), Dr Débora Pires (Museu Nacional – UFRJ), Dr Marymegan Daly (Ohio State University), Dr Stephen Cairns and Dr Allen Collins (Smithsonian National Museum of Natural History), Dr Gustav Paulay (Florida Museum Science), Dr Fabrizio Scarabino (Centro Universitario Regional Este UDELAR), Dr Kennet Lundin (Göteborgs Naturhistoriska Museum), Dr Antonio Carlos Marques and Dr Alvaro E Migotto (Universidade de São Paulo), Dr Marcelo V Kitahara (Universidade Federal de São Paulo), Dr Victor Quintino and Dr Ana Rodriguez (Universidade de Avero), Dr Mark Vermeij (Caribbean Research and Management of Biodiversity), Dr Mark Gibbons (University of the Western Cape), Dr Adam Reitzel (University of North Carolina at Charlotte), Dr Jason Macrander (Florida Southern College), Dr Shin Kubota (Seto Marine Biological Laboratory), and Dr Andreja Ramsak (National Institute of Biology, Slovenia)). We are also grateful to the two reviewers and Dr Bert Hoeksema (Subject Editor) who provided constructive comments on an earlier version of this manuscript. This is a publication of NP-BioMar-USP.

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